



IMPERIAL AGRICULTURAL
RESEARCH INSTITUTE, NEW DELHI.

Bulletin

of the

Torrey Botanical Club

VOLUME 63

FOUNDED BY WILLIAM HENRY LEGGETT 1870

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NEW YORK

1936

Published for the Club
GEORGE BANTA PUBLISHING COMPANY
Menasha, Wisconsin

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Dates of publication

- No. 1, for January, pages 1-52, issued January 2, 1936
No. 2, for February, pages 53-114, issued February 1, 1936
No. 3, for March, pages 115-176, issued March 3, 1936
No. 4, for April, pages 177-236, issued April 1, 1936
No. 5, for May, pages 237-306, issued May 4, 1936
No. 6, for June, pages 307-364, issued June 2, 1936
No. 7, for October, pages 365-428, issued October 1, 1936
No. 8, for November, pages 429-494, issued November 2, 1936
No. 9, for December, pages 495-562, issued December 16, 1936

Errata

- Page 46, 19th line, for *Zephranthes*, read *Zephyranthes*.
Page 237, 7th line from bottom, and page 256, third line from bottom, for *americana*, read *americanum*.
Page 237, 14th line; page 245, 6th line, and 4th line from bottom; page 246, 17th line; and page 254, last line, for *Alcyonidiae*, read *Alcyonidii*.
Page 247, 9th line from bottom, and page 256, 5th line, for *Ensisae*, read *Ensis*.
Page 344, 6th line from bottom, for *Elaphyrum*, read *Elaphrium*.

Polarized growth and cell studies on the *Avena* coleoptile, phytohormone test object

GEORGE S. AVERY, JR. AND PAUL R. BURKHOLDER

(WITH SIX FIGURES)

INTRODUCTION

Our knowledge of plant hormone activity has grown up chiefly through studies made upon the growth and tropisms of the *Avena* coleoptile. Experiments in which known amounts of growth hormone (contained in agar blocks) were placed upon decapitated coleoptiles, have shown that within certain limits, growth intensity is proportional to the concentration of the hormone, (Went, 1928; Thimann and Bonner, 1933). It would appear, therefore, that its natural distribution in plants is causally associated with growth patterns of developing organs. This has been demonstrated in a preliminary way in *Avena* coleoptiles (Thimann, 1934) and in *Nicotiana* leaves (Avery, 1935), where zones of more rapid increase in length have been shown to possess greater amounts of the hormone.

The gross morphological structure and development of the *Avena* coleoptile (standard test object in the quantitative determination of plant hormones) are moderately well understood, but comparatively little attention has been given to the cell and tissue changes involved in its growth and development. Since no mitoses were found in prepared sections of the growing coleoptile (Tetley and Priestley, 1927), observers have concluded that this second leaf of the oats seedling grows almost entirely by the enlargement of cells already present (laid down during embryogeny). Observations made on the number of cells in the epidermis of the growing coleoptile (*Zea* and *Avena*) showed that these cells actually do not multiply (Tetley and Priestley, 1927), although the over-all length of the coleoptile may increase many fold. This information, together with other data, led to the generally accepted conclusion that growth hormones are involved solely in cell elongation.

The fact that cell division was found in the rapidly elongating basal portion of the *Nicotiana* leaf where the auxin concentration was high, suggested a possible rôle of the hormone in cell division (Avery, 1935). Furthermore, pure "heteroauxin" has been demonstrated to promote cell division in the cambium (Snow and LeFanu, 1935), and in callus tissue (Laibach, Mai, and Müller, 1934). In the light of these discoveries it seemed possible that cell division, as well as cell elongation, might be contributing to growth of the *Avena* coleoptile.

MATERIALS AND METHODS

Avena sativa seeds of the pure line "Siegeshafer" were obtained from Dr. E. Å. Åkerman of Svalöv, Sweden. The wheat used was *Triticum vulgare* var. Marquis, supplied by the U. S. Department of Agriculture,

TABLE 1

Avena. Segment size and ratio of segment growth to that of the coleoptile as a whole in successive stages of its development.

STAGES (SEGMENT LENGTHS IN MM.)		I		II		III		IV		V
GROWTH RATIOS IN STAGE INTERVALS			I-II		II-III		III-IV		IV-V	
	Series									
<i>a</i> segment	1	1	.57	1.69	.68	1.93	.75	2.08	.88	2.34
	2	1	.73	1.85	.68	2.16	.76	2.52	.88	3.20
	3	1	.62	1.69	.53	2.02	.93	2.66	.85	2.71
	4	1	.63	1.45	.51	1.83	.93	2.70	.96	2.95
<i>b</i> segment	1	1	1.00	2.98	.89	4.70	.91	6.56	1.18	8.72
	2	1	1.10	2.80	.97	4.68	1.00	7.20	1.10	11.40
	3	1	.97	2.66	.95	5.72	1.06	8.57	1.06	10.88
	4	1	.98	2.24	.93	5.22	1.10	9.09	1.14	11.81
<i>c</i> segment	1	1	1.11	3.31	1.06	5.87	1.08	9.20	1.06	12.49
	2	1	1.16	2.95	1.16	5.89	1.08	9.79	1.22	13.70
	3	1	1.10	3.00	1.14	7.78	1.02	11.20	1.08	14.50
	4	1	1.14	2.61	1.13	7.37	1.09	12.70	1.02	14.79
<i>d</i> segment	1	1	1.29	3.93	1.13	7.41	1.02	10.96	.94	13.12
	2	1	1.00	2.57	1.08	4.80	1.00	7.36	.98	10.40
	3	1	1.34	3.58	1.15	9.35	.97	12.82	.91	14.00
	4	1	1.26	2.89	1.18	8.54	.88	11.90	.88	12.06

Number of plants and average over-all length of coleoptiles in the four experimental series given above.

SERIES	NUMBER OF PLANTS	DEVELOPMENTAL STAGES				
		I	II	III	IV	V
1	32	4	11.91	19.91	28.80	36.67
2	18	4	10.17	17.53	26.87	38.70
3	20	4	10.93	24.87	35.25	42.09
4	16	4	9.19	22.96	36.39	41.61

Washington, D. C. Seeds were soaked in tap water for several hours and then were placed upon moist filter paper in glass germinating dishes and kept in diffuse light in the laboratory for one day. Further germination and growth took place in a dark room, lighted for intermittent observations only with phototropically inactive ruby glass Mazda lamps. During

the early period of germination the seedlings adhering to the moist filter paper were kept in a nearly vertical position in order to avoid growth curvatures which might have taken place due to geotropic stimulation. When the coleoptiles attained a length of 4 mm., those that were uniform were placed in specially constructed glass holders which permitted erect growth of the coleoptile. The plants were grown in tap water. A fine camel's hair brush and powdered carbon black suspended in lanolin were used for marking the coleoptiles into segments, under a binocular microscope. Subsequent growth took place in a moist thermostatic chamber where the relative humidity was about 90% and the temperature was approximately 26°C.

TABLE 2

Triticum. Segment size and ratio of segment growth to that of the coleoptile as a whole in successive stages of its development. The data represent averages of a total of 17 plants.

STAGES (SEGMENT LENGTHS IN MM.)	I		II		III		IV		V
GROWTH RATIOS IN STAGE INTERVALS		I-II		II-III		III-IV		IV-V	
<i>a</i> segment	1	.69	1.69	.76	2.32	.70	2.98	.96	3.94
<i>b</i> segment	1	.96	2.35	.98	4.19	.91	7.02	1.14	11.22
<i>c</i> segment	1	1.05	2.57	1.07	4.98	1.08	9.93	1.11	15.44
<i>d</i> segment	1	1.31	3.22	1.09	6.37	1.11	13.07	.86	15.84
Average over- all coleoptile length in millimeters	4		9.83		17.86		33.00		46.44

Details of the experiments follow, but it should be mentioned here that one inherent difficulty lay in estimating the exact position of the basal end of the coleoptile. Some of the plants which were marked later gave clear indication of inaccurate marking, the lanolin having been applied either just above or below the coleoptilar node. Only those coleoptiles which grew straight and gave evidence of having been marked correctly at the 4 mm. stage were kept for later observations. Subsequent measurements were made to tenths of a millimeter under a binocular microscope. The experiments on *Avena* were repeated four times. Series I was made up of 32 plants; series II, 18 plants; series III, 20 plants; and series IV, 16 plants (table 1). In a similar study of *Triticum* 17 uniform plants were carried through from germination to maturity of the coleoptiles (table 2).

At different stages of growth from the embryo to maturity, a certain number of representative coleoptiles were selected, cut into segments and

preserved for microscopic study. In preliminary trials with formol-acetic-alcohol, Carnoy's and Nawaschin's fluids, the best results were obtained in the last named fixing solution. The usual steps were followed in dehydration and paraffin infiltration, and longitudinal sections were cut at thicknesses ranging from 10 to 24 microns. Crystal violet was used for staining.

Examinations of the slides gave indication of differential shrinkage of the segments, and further observations showed that most of this shrinkage took place during dehydration and paraffin infiltration. The tip of the coleoptile (segment *a*, fig. 1) was subject to almost no shrinkage, whereas

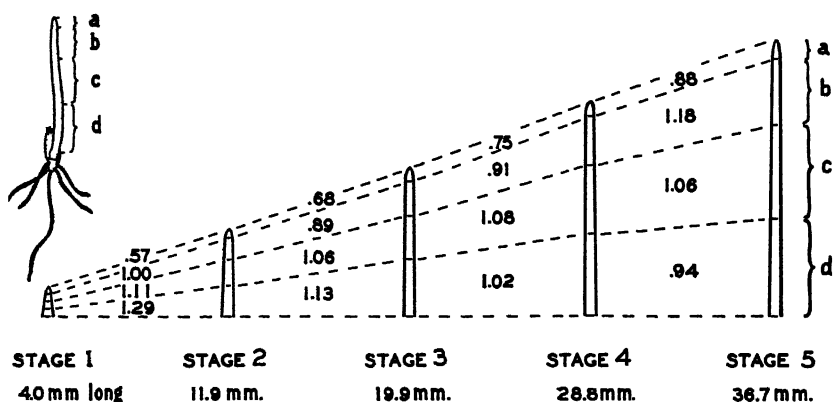


Fig. 1. Diagrams of the *Avena* coleoptile at different stages of development. Coleoptiles 4 mm. long (stage I) were marked into four 1 mm. segments (*a*, *b*, *c*, *d*), and the length of each was measured in several later stages of growth. The figures between stages indicate the ratio of the increase in segment length to increase in the length of the coleoptile as a whole (see text). Most of the increase in coleoptile length is due to greater relative elongation of segments *b*, *c*, and *d*. Note that the growth of segment *a* relative to the coleoptile as a whole increases as the coleoptile grows older, while the relative growth rate of segment *d* decreases with age. Data from table 1, series 1.

in segments *c* and *d*, shrinkage was often as much as 10%. Due to the differential shrinkage in length of the prepared sections, in contrast with the living tissues, it was not possible to determine cell lengths without making necessary corrections for this shrinkage.

The number and size of the cells in each segment were obtained for all the stages in coleoptile growth. Due to the extreme elongation of the epidermal cells and the consequent difficulties of obtaining full length median sections, it was necessary to use living material for observations on this layer.

The embryonic coleoptiles (fig. 3) were not marked and cut into seg-

ments before sectioning. Their over-all length was divided into four equal parts, corresponding to segments *a*, *b*, *c*, and *d* of the later stages. The cells were measured and counted in each layer (epidermis, subepidermis, etc.) of each segment. From these data it was possible to ascertain to what extent cell multiplication and cell elongation participated in the growth of the coleoptile.

DIFFERENTIAL GROWTH RATES

In order to determine relative growth rates in different portions, growing coleoptiles 4 mm. in length were marked off into four 1 mm. segments, and the length of each was measured in several later stages of development. The *ratio* of the increase in segment length to increase in the length of the coleoptile as a whole, i.e., "k," was then determined for each growth period as follows:

$$\begin{aligned} \text{"k,"} &= \frac{\text{segment length stage}_2}{\text{segment length stage}_1} \\ &= \frac{\text{coleoptile length stage}_2}{\text{coleoptile length stage}_1} \\ \text{or, "k,"} &= \frac{\text{segment growth}}{\text{coleoptile growth}} \end{aligned}$$

Example: The mean length of segment *a*, stage IV, is 2.08 mm., and this increases to 2.34 mm. in stage V. Meanwhile the average length of the coleoptile increases from 28.80 mm. to 36.67 mm. The growth of the segment may be expressed as follows:

$$\frac{\text{segment } a_V \ 2.34}{\text{segment } a_{IV} \ 2.08} = 1.125,$$

and the increase of the whole coleoptile may be stated as:

$$\frac{\text{coleoptile}_V \ 36.67}{\text{coleoptile}_{IV} \ 28.80} = 1.274$$

Then, $\frac{\text{segment growth of } 1.125}{\text{coleoptile growth of } 1.274} = 0.884 = \text{"k,"}$ or, the segment growth rate = .884 \times coleoptile growth rate.

Such calculations yield simple quantitative expressions of differences in the growth rate of various segments of the coleoptile relative to its growth as a whole, at different periods of its development. If "k" for a particular segment between any two stages = 1, it indicates that the segment is increasing in length at the same rate as the coleoptile as a whole; if less than 1, that the segment is growing at a slower rate than the structure

as a whole, or, if greater than 1, proportionally greater than the coleoptile as a whole.

Figure 1 shows five stages in the development of the coleoptile. Segment *a* is growing relatively more rapidly as the coleoptile matures (0.57, 0.68, 0.75, 0.88). In the last stage of coleoptile elongation, segment *a* is growing about 88/100 as rapidly as the organ as a whole. The figures for intermediate stages of the elongation of segment *b* do not show successive increases, but it is clear that the segment is growing more rapidly toward the end of its development than in the beginning; segments *a* and *b* are similar therefore in speeding up their relative growth rate as the coleoptile nears maturity. Segment *c* elongates at a rate about equal to that of the coleoptile as a whole, and maintains this rate throughout development. Segment *d*, in contrast to the behavior of the upper segments, grows relatively more slowly as the coleoptile elongates. The decrease in relative growth rate of this segment is compensated for by the acceleration of segments *a* and *b*.

The shift in position of the zone of maximum growth rate is more graphically shown in figure 2. As the coleoptile approaches maturity, growth slows down throughout its length, ceases at its base, and becomes relatively greater near its apex. After the leaf bursts through, growth is even more sharply localized in the tip segment.

CELL NUMBER AND SIZE

The number and size of the cells in the epidermis, subepidermis, third layer, fourth layer and the inner epidermis were determined in median longitudinal sections for each of four segments at six stages in the growth of the coleoptiles of *Avena* and *Triticum*. The vascular tissues were not included in this study. Determinations of average cell number in each layer in the *Avena* coleoptiles are presented in table 3 and in figure 5. Similar data for *Triticum* are given in table 4. The number of epidermal cells in the coleoptile remains constant from the embryo to maturity. It is about thirty cells from tip to base in the embryonic condition, and

Fig. 2. *Avena* coleoptile. Diagrams to show shift in position of the zone of maximum growth intensity. Coleoptiles were marked as indicated at the left, and in the upper four experiments were allowed to grow until the time when the foliage leaf ordinarily bursts through. The individual segments were then measured and the percentage increase in length was determined for each. The latter is indicated in the right hand column. The density of the dots as well as the percentage figures indicate growth intensity and the shift in the region of maximum growth from the base in the young coleoptile to the apical region in maturing coleoptiles. Growth is slowing down throughout while this change is taking place. Each diagram represents data from a single coleoptile selected as typical from a group of at least three similarly marked.

TABLE 3

Avena. Cell number in different portions (tip to base) of the coleoptile in successive stages of its development. Stages I, II, III, IV and V represent averages of 3 to 5 coleoptiles each, stage VI, 13 coleoptiles.

STAGES (OVER-ALL LENGTH OF COLEOPTILES)		I ¹ (1.62 mm.)	II (4 mm.)	III (9.83 mm.)	IV (17.86 mm.)	V (33 mm.)	VI (46.44 mm.)
a segment ²	Length in mm.	0.41	0.9	1.8	1.9	2.6	2.5
	Epidermis	7	8	9	7	7	7
	Subepidermis	12	26	34	29	32	30
	3rd layer	11	25	33	29	33	29
	4th layer		25	32	27	26	27
	Inner epidermis	8	19	20	20	19	22
b segment	Length in mm.	0.41	0.9	2.4	5.2	8.2	11.2
	Epidermis	7	6	7	5	6	7
	Subepidermis	15	34	47	62	55	57
	3rd layer	16	31	41	51	46	51
	4th layer		28	35	46	43	43
	Inner epidermis	12	21	25	33	33	30
c segment	Length in mm.	0.41	0.9	2.9	7.1	10.7	13.1
	Epidermis	8	6	7	5	7	6
	Subepidermis	16	37	55	57	57	58
	3rd layer	18	32	47	52	50	52
	4th layer		28	41	46	41	46
	Inner epidermis	15	26	33	39	42	40
d segment	Length in mm.	0.41	0.9	3.2	6.2	11.4	12.6
	Epidermis	11	9	8	6	8	6
	Subepidermis	17	32	48	44	47	50
	3rd layer	16	30	42	44	43	44
	4th layer		27	40	38	41	38
	Inner epidermis	16	29	41	36	35	37
Totals	Epidermis ³	33	29	31	23	28	26
	Subepidermis	60	129	184	192	191	195
	3rd layer	61	118	163	176	172	176
	4th layer		108	148	157	151	154
	Inner epidermis	51	95	119	128	129	129

¹ Embryos which had been soaked for 24 hrs. were used in stage I. Actual length of the dormant embryos (average of 5)=0.67 mm.

² 1/10 of tip not counted because, *first*, that portion of the segment does not elongate as does the balance of the segment, and *second*, all the active cell layers in which cell counts were made do not continue on into the tip.

³ The actual epidermal cell counts from tip to base of coleoptile including the 1/10 excluded above in segment a, are as follows for the six stages respectively: 34, 32.4, 35.2, 28.5, 32.5, 31.2.

TABLE 4

Triticum. Cell number in different portions (tip to base) of the coleoptile in successive stages of its development. Data taken from an average of 2 to 5 coleoptiles for each stage.

STAGES (OVER-ALL LENGTH OF COLEOPTILES)		I ¹ (0.76 MM.)	II (3.9 MM.)	III (10.2 MM.)	IV (17.79 MM.)	V (32.61 MM.)	VI (40.35 MM.)
<i>a</i> segment ²	Length in mm.	0.19	0.90	1.58	1.88	2.48	3.60
	Epidermis	7	12	8	10	8	13
	Subepidermis	8	22	22	21	17	23
	3rd layer	9	18	21	21	21	20
	4th layer		22	21	20	21	24
	Inner epidermis	8	11	12	13	12	13
<i>b</i> segment	Length in mm.	0.19	1.00	2.38	4.33	7.13	10.75
	Epidermis	9	8	8	10	9	8
	Subepidermis	11	32	39	41	47	54
	3rd layer	12	23	33	37	38	41
	4th layer		24	35	36	38	40
	Inner epidermis	12	11	13	17	18	20
<i>c</i> segment	Length in mm.	0.19	1.00	2.75	5.08	11.00	11.00
	Epidermis	11	10	10	13	14	8
	Subepidermis	12	36	57	56	65	74
	3rd layer	12	34	48	48	58	57
	4th layer		33	48	49	51	63
	Inner epidermis	13	16	18	20	25	27
<i>d</i> segment	Length in mm.	0.19	1.00	3.50	6.50	12.00	15.00
	Epidermis	14	12	16	12	13	15
	Subepidermis	11	33	51	48	57	67
	3rd layer	12	26	53	49	50	61
	4th layer		26	54	47	48	61
	Inner epidermis	13	20	29	29	29	29
Totals	Epidermis ³	41	42	42	45	43	44
	Subepidermis	42	123	169	166	186	218
	3rd layer	45	101	155	155	167	179
	4th layer		105	158	152	158	188
	Inner epidermis	46	58	72	79	84	89

¹ The embryo (dry) was used as stage I.

² 1/10 of tip not counted because, *first*, that portion of the segment does not elongate as does the balance of the segment, and *second*, all the active cell layers in which cell counts were made do not continue on into the tip.

³ The actual epidermal cell counts from tip to base of coleoptile including the 1/10 excluded above in segment *a*, are as follows for the six stages respectively: 42, 48, 44, 46, 47, 44.

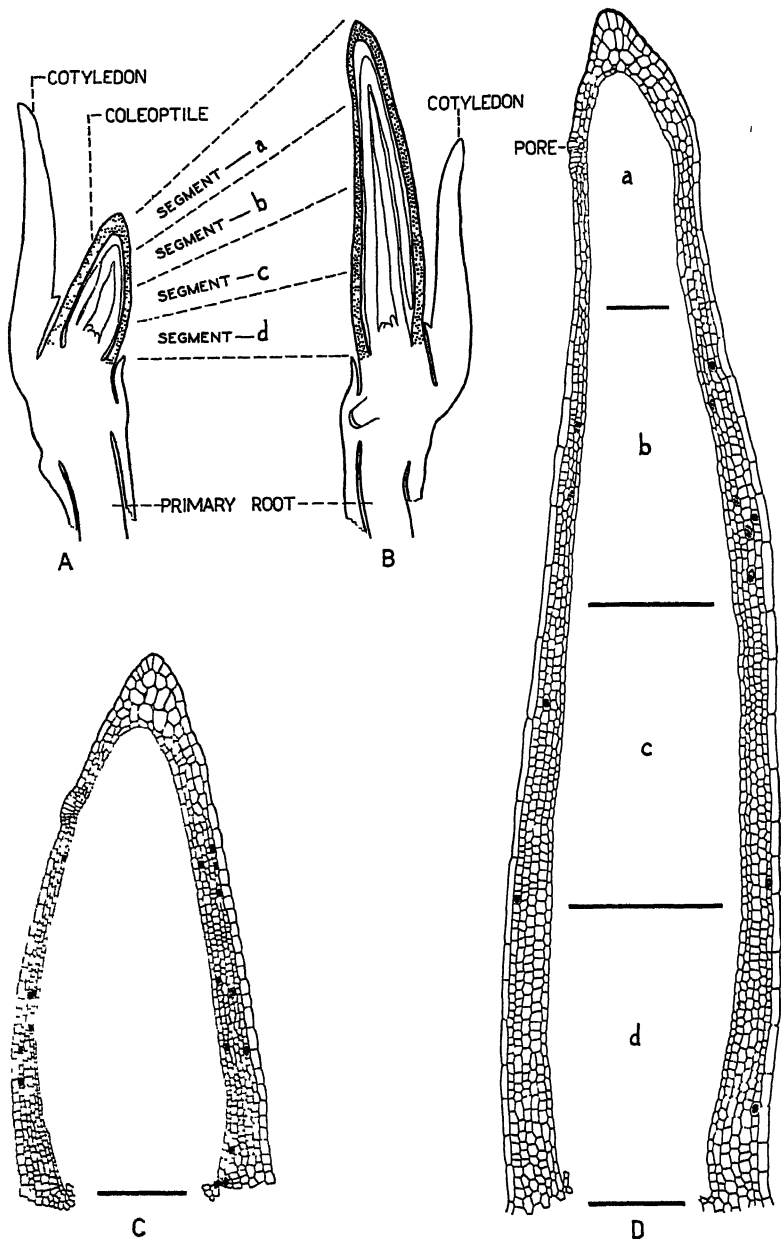


Fig. 3. A and B, diagrams of median longitudinal sections through germinating embryos of *Avena* at two different ages, $\times 40$. In these two stages (I and II, table 3) of development, the coleoptile was divided into 4 segments of equal length. C and D, detailed drawings of the coleoptiles of the above embryos (1.62 and 4 mm. long, respectively), with segments indicated by heavy lines. Mitoses are evident throughout. Cell number determinations (stages I and II, table 3) in the epidermis, subepidermis, third layer, fourth layer and inner epidermis of the different segments were made from such sections.

grows to maturity without any increase in cell number. This means that the cells of the outer epidermal layer keep pace in their elongation with the growth of the coleoptile. At maturity these very long thin cells attain in some instances a length of 3 mm., an increase of 150 times their embryonic "length".

The other layers (subepidermis, third layer, fourth layer and inner epidermis) show a considerable increase in the number of their constituent cells (in the long axis of the coleoptile), especially during the first quarter of the growth period. In segment *a* at the tip of the coleoptile, there is less

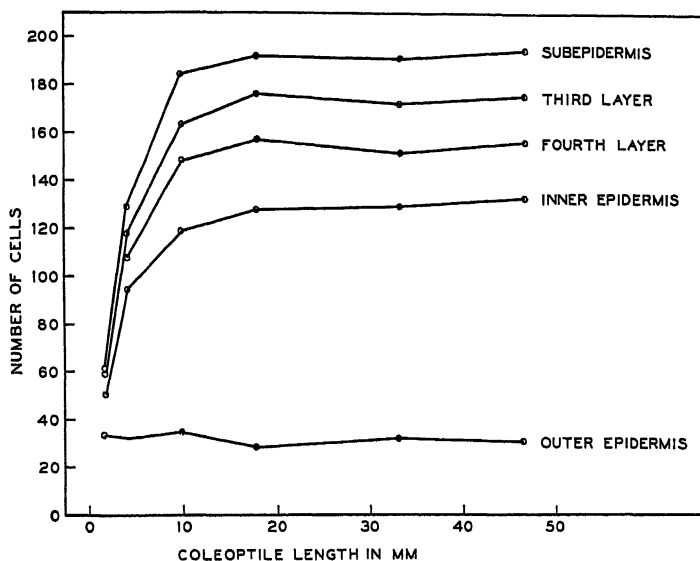


Fig. 5. Graph showing the number of cells from tip to base in the different layers of the *Avena* coleoptile, at six stages in its growth. Although the outer epidermal cells do not increase in number, the cells of the other layers multiply rapidly in the early period of development and then remain about constant in number. A definite gradient of cell-division intensity, decreasing inward from the subepidermis to the inner epidermis, is apparent for the first quarter of the growth period. During the last three quarters of its growth, elongation of the coleoptile is proportional to the elongation of all its constituent cells. Substantially similar results were obtained for *Triticum* (table 4).

cell division than in the other segments. The cells in the region above the tips of the vascular bundles, i.e., from the pore upward (figs. 3, 4), undergo neither elongation nor division.

When the total number of cells from tip to base in each layer is plotted against coleoptile length at each stage (fig. 5), the differential behavior of the various layers of parenchyma becomes evident. From the embryonic stage up to the time when the leaf bursts through the coleoptile, the

number of cells in the subepidermis increases 3.2 times, in the third layer 2.9 times, and the inner epidermis, 2.5 times; i.e., there is a distinct gradient from the subepidermis inward.

Embryo and mature coleoptiles were examined in transverse section at the base. There was no increase in the number of cells (fig. 6). Increase in cell number as well as cell elongation are taking place, only in the long axis of the organ, i.e., growth is distinctly *polarized*.

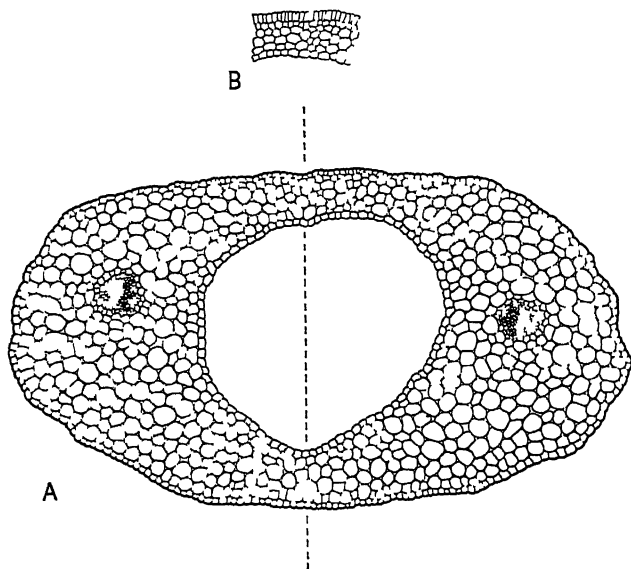


Fig. 6. A, transverse section of the lowermost end of a mature *Avena* coleoptile, $\times 40$; B, transverse section of the narrow portion of the base of a 2 mm. long coleoptile. The number of cells is the same in transverse sections of young and old coleoptiles. The drawings for fig. 4 were made from sections cut in the plane indicated by the broken line.

DISCUSSION

Rothert (1894) first observed a shift in the zone of most rapid elongation in the growing coleoptile of *Avena*. He noted that maximum growth was taking place near the base in coleoptiles up to 12–15 mm. in length. In older plants growth had decreased at the base and the zone of most rapid elongation lay in the region about 10 mm. below the tip. These observations together with the results of more recent investigations on older coleoptiles (Went, 1928; Bonner, 1933), have led to the generally accepted conclusion that the lower zones grow more slowly than those nearer the tip. The experiments reported here, however, have shown that growth is

mainly basal during the period when the coleoptile is achieving the greater part of its length. In fact, it has been shown that the lower half of a 4 mm. coleoptile is responsible for nearly $\frac{3}{4}$ of the subsequent elongation. Relatively little growth in total length may be attributed to the region of maximum growth rate when it lies near the tip.

Söding (1929) investigated the distribution of growth hormone at different levels in *Avena* coleoptiles grown in the light; it was most abundant in the upper 1 mm., and decreased gradually downward until none could be demonstrated at the base. The tips of old coleoptiles, which have been broken through by the foliage leaf, contain little or no hormone.

In attempting to correlate hormone concentration with growth intensity, Thimann (1934) made extracts of successive segments from the apex downward in 26 mm. coleoptiles. Successively lower zones were successively less rich in the hormone. The tip 1 mm. segment was found to be $3.6\times$ richer than the 1 mm. segment at the base. Hormone gradients have not been reported for coleoptiles in other stages of development. Laibach and Meyer (1935), however, found a high auxin content in seeds of *Zea*, the concentration falling off rapidly with germination. These facts suggest that auxin may be moving upward from the endosperm and cotyledon through the vascular bundles to the tip of the coleoptile from which point it is dispersed downward. Gradual depletion of the auxin supply might explain the decrease in growth rate and the acropetal migration of the maximum growth zone as the coleoptile nears maturity.

Bonner (1933) placed segments taken from the tips and bases of coleoptiles in solutions of the growth hormone. Segments from the upper third of the coleoptile showed a growth response more than twice as great as that of the lower segments. If these coleoptiles were 25–30 mm. long or longer (length not given), their degree of maturity at different levels as shown here, would explain the differential growth vigor of the isolated segments. It is probable that mature tissues near the base are incapable of growth when the food supply is exhausted (Went, 1935), even in the presence of favorable concentrations of the hormone. Furthermore, Went has shown that auxin becomes a limiting factor in the later stages of coleoptile growth. By the addition of more auxin, the ability to utilize the stored food in polarized growth is continued for a longer time.

The use of the *Avena* coleoptile as a quantitative test object for auxin has been based on the assumption that the hormone brings about increase in length only by cell elongation. It has been shown here that cell division takes place in the early stages of coleoptile growth, but this cell division ceases relatively early so that by the time the coleoptile is used for auxin tests, its elongation is directly proportional to the growth in length of its

constituent cells. Its use as a quantitative test object for hormones causing cell stretching is, therefore, valid.

SUMMARY

Determinations of relative growth rates on coleoptiles of *Avena* show the following:

1. The lower half of the embryonic coleoptile elongates to make up approximately three-fourths of the total length of the mature coleoptile. The upper half of the embryonic coleoptile elongates to make up the upper one-fourth of the mature coleoptile.

2. Although growth is taking place rapidly throughout the length of the coleoptile while it is young, the region of greatest elongation is basal. As the coleoptile nears maturity, growth slows down throughout its length, ceases at its base, and becomes *relatively* greater near its apex. At the time the foliage leaf bursts through, all basal growth has ceased, but a localized elongation region still remains at the tip, and this may persist for as much as 2 or 3 days after the leaf bursts through the coleoptile.

Cell counts and measurements on longitudinal median sections of growing coleoptiles show the following:

1. The number of epidermal cells remains the same throughout the growth period, i.e., on the average, their elongation is directly proportional to that of the coleoptile as a whole. The length of some of these cells increases as much as 150 times.

2. While the outer epidermal cells are elongating, the underlying parenchyma and inner epidermal cells on the average increase their number 2.9 times. At maturity the greatest number of cells is in the subepidermis, and each successive layer inward has fewer cells. This means that there have been fewer cell divisions in each successive layer inward from the subepidermis.

3. Most of the increase in numbers of cells takes place by the time the coleoptile is 1 cm. long, or about one-fourth of its final length. In this period the coleoptile increases in length as much as 14.7 times, while the gain in number of cells is 172%, or 2.7 times. In the balance of the growing period, up to maturity, the coleoptile increases in length as much as 4.6 times, while cell number gains only 7%, or 1.07 times. This further slight increase in numbers of cells takes place before the coleoptile is 18 mm. long. There is neither cell division nor cell enlargement in the tip between the pore and the apex. The increase in cells takes place below the pore and is about evenly distributed throughout.

4. Transverse sections of embryonic and mature coleoptiles show no appreciable difference in diameter, nor is there any increase in the number

of cells. Cell elongation and the increase in cell number take place only in the long axis of the organ, i.e., growth is *polarized*.

5. From (3) it is reasonable to conclude that cell division is not involved in coleoptile growth at the time it is used for growth hormone tests (Went technique). Growth in the later stages is directly proportional to the stretching of cells.

6. There is a brief discussion of the probable relationship between changing growth intensity and auxin concentration in the coleoptile.

The data given for growing coleoptiles of *Triticum* are substantially the same as for *Avena*.

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Cell size and organ size in two violet species and their hybrid¹

J. W. MARVIN

(WITH PLATE 1 AND SEVEN TEXT-FIGURES)

INTRODUCTION

An attempt to analyze the morphogenesis of an organ in terms of a summation of the development of its parts presupposes a more complete knowledge than we possess. Of the many cell and organ relationships, that of cell size to organ size was early recognized as important.

In metaphytes the achievement of organ size is a two-fold process—namely, the result of the auxesis and the meresis of the cells of the *Anlagen* accompanied by differentiation and physiological specialization. It seems significant that, in differentiated and mature tissue, cell size becomes fixed within certain limits and is a relatively constant character, as was suggested by Sachs (1877). Amelung (1893) showed it to be true for organs of different sizes on the same plant individual and on closely related plant individuals.

A study of some of the organs of a violet species hybrid and its parents shows the hybrid organ to have a specific cell size different from that of either parent. And further, depending upon the organ studied, the size of the cells in the hybrid organ may or may not be intermediate between the sizes of the cells of each of the parent organs.

LITERATURE REVIEW

Sachs' (1877) conception that there is a relatively constant cell size for a species was confirmed by Amelung (1893), Sierp (1913), Sinnott (1930), and many others.

Amelung measured cells from comparable regions on mature organs of the same plant individual. He found that cell size was relatively constant and that differences in organ size were due to a difference in the number of cells. He measured epidermal and palisade parenchymal cells as well as wood cells and fruit parenchymal cells. He found that a small leaf of *Ficus macrocarpa* had epidermal cells which were nearly the same size as the epidermal cells of a leaf twice as large. Also, the palisade parenchymal cells from a small leaf of *Buxus sempervirens* were of essentially the same size as cells from a leaf three times as long and three times as broad. Measurements of pith cells from different sized stems of *Sambucus niger*

¹ This investigation was carried on at the Vermont Agricultural Experiment Station, and the results are published with the permission of the Director, Dean J. L. Hills.

gave slightly different results. In a comparison of a long stem having a large diameter with a short stem having a small diameter, the large stem had pith cells which were considerably larger than those in the small stem.

Amelung also measured cells from comparable regions of mature organs on different plant individuals belonging to different genera of the same family. He compared palisade parenchymal cells from the large leaved *Rheum officinale* with those from the small leaved *Polygonum cuspidatum*. The area of the large leaf (*R. officinale*) was approximately fifty times greater than that of the small leaf (*P. cuspidatum*). This comparison showed the large leaf to have cells which were approximately 20% greater than those of the small leaf. Other similar comparisons did not show such marked results.

Tenopyr (1918) found that leaves of different shapes on the same plant individual were composed of cells of the same or of nearly the same shape. The ratio between the length and the width of basal orbicular leaves of *Campanula rotundifolia* was 0.92:1; the constituent epidermal cells had a length to width ratio of 1.02:1. Linear leaves from the stem with a length to width ratio of 14.15:1 possessed epidermal cells with a length to width ratio of 1.07:1.

She compared cells from different shaped leaves which were taken from two species of plantain, *Plantago major* and *P. lanceolata*. The ratio of leaf length to leaf width in *P. major* was 1.6:1, and the ratio between the length and the width of the lower epidermal cells was 0.75:1. In the case of *P. lanceolata* the length to width ratio of the entire leaf was 9.2:1, while the epidermal cells had a length to width ratio of 0.85:1. Thus leaves of different shapes from closely related plant individuals were also found to be composed of cells of nearly the same shape.

And further, she found that the average cell size for an organ in the mature condition was relatively constant for a species. This size may vary considerably, however, depending upon the stage of development of the plant at the time the organ was produced.

Sinnott (1930) has shown recently in an investigation of the length to width ratio of cells from different tissues of an organ that the cells do not respond in the same way to elongation of the organ. In a comparison of large and small petioles of *Acer saccharum*, he found that an increase in petiole diameter was accompanied by an increase in the size of the pith cells, and that an increase in petiole length was accompanied by an increase in pith cell size and number. There was, however, no correlation between epidermal cell size and organ size.

Lutman (1934) working on meristematic and mature differentiated

tissue shows that the lack of certain inorganic elements may stimulate early senescence and have a marked effect on cell size. He grew Japanese millet, rape, buckwheat, and garden beets in sand cultures using nutrient solutions in which either nitrogen, phosphorus, magnesium, potassium, or calcium was lacking. In other cultures these elements were in turn supplied in excess. Lutman found that the meristematic, undifferentiated cells of the root tips in millet, rape, and buckwheat which were grown in cultures lacking either nitrogen, phosphorus, magnesium, potassium, or calcium were prematurely vacuolate, had a reduced amount of stored food, and small nuclei. Each of these conditions is a sign of early senescence. Cells of the leaf epidermis of the same plants grown in solutions which lacked several of the so-called essential elements were smaller than comparable cells from plants grown in a complete culture solution. Further, the small cell size was correlated with the small size of the plant organs from which the cells were taken. A superabundance of any element used gave nearly the same results as the complete nutrient solution.

Macfarlane (1892), in an extensive study of many hybrids and their parents, considering external and internal morphology, found the hybrid to be an intermediate expression. He compared size, number, and position of hairs, the amount of cuticular deposit, the leaf venation, and the amount of secondary thickening in the parents and their hybrids. Reichert (1919) worked on starch grains in many different plants. He found, in a comparison of starch grains from parents and hybrids, that, while the hybrid starch grains were often intermediate, in many cases, they favored one or the other parent. Paulesco (1900) studied the morphology and anatomy of various spontaneous species hybrids (*Sorbus aria* × *S. aucuparia*, *Cistus longifolius* × *C. populifolius*, *Viola arenaria* × *V. riviniana*, *Viola mirabilis* × *V. sylvatica*, etc.) and their parents. He found that in many cases the hybrid characters were an intermediate expression. In other cases "juxtaposition" of some of the characters of each parent occurred; in still others he finds the hybrid to resemble very closely one of the parents.

MATERIALS AND METHODS

The plants used in these studies were collected from stock grown as part of the extensive violet project of the Vermont Agricultural Experiment Station. The parent species are inbred and are uniform strains which have been grown in the greenhouse for several years. In 1929 plants of *Viola conspersa* were pollinated with plants of *Viola papilionacea* by Dr. A. Gershoy. Several vigorous, sterile hybrid plants were obtained as a result of this cross, and these have since been propagated by mechanical division.

Material for histological study was fixed in chrom-acetic acid. It was found necessary to use the butyl alcohol method to prevent undue hardening of the tissue in imbedding. The sections were stained with either iron alum-haematoxylin or Flemming's triple stain.

The cells studied were drawn with a camera lucida at a magnification of 725 diameters. The areas of these cells were determined by the use of a planimeter. The readings, in square millimeters, were then converted into square microns. For each tissue studied, over two hundred cells of each parent and of the hybrid were measured. The arbitrary selection and measurement of cells from the regions studied is open to criticism, since some of the areas measured may not have been median sections of cells but rather, near one of the faces. The measurements, therefore, do not necessarily represent precisely the so-called specific cell size; they are comparable, however, and therefore are considered significant in this study.

Some difficulty was encountered in selecting comparable regions of the cortex, because, at the apex, there is little internodal stretching and the spirally arranged nodes are very close together. Since it was necessary for the purpose of this study to select a region in which the cortical cells were still nearly isodiametric and at the same time had attained maximum width before there occurred an appreciable stretching involved in the internode elongation, the cells in the first internode of appreciable elongation, below the apex, and near a branch meristem, were selected. The epidermal cells were taken from the upper epidermis of freshly gathered mature leaves from the basal portion of the stem. Hand sections were obtained from between large veins as near the center of the leaf blade as possible. These sections were mounted in glycerin and the areas of the cells computed.

OBSERVATIONS AND DATA

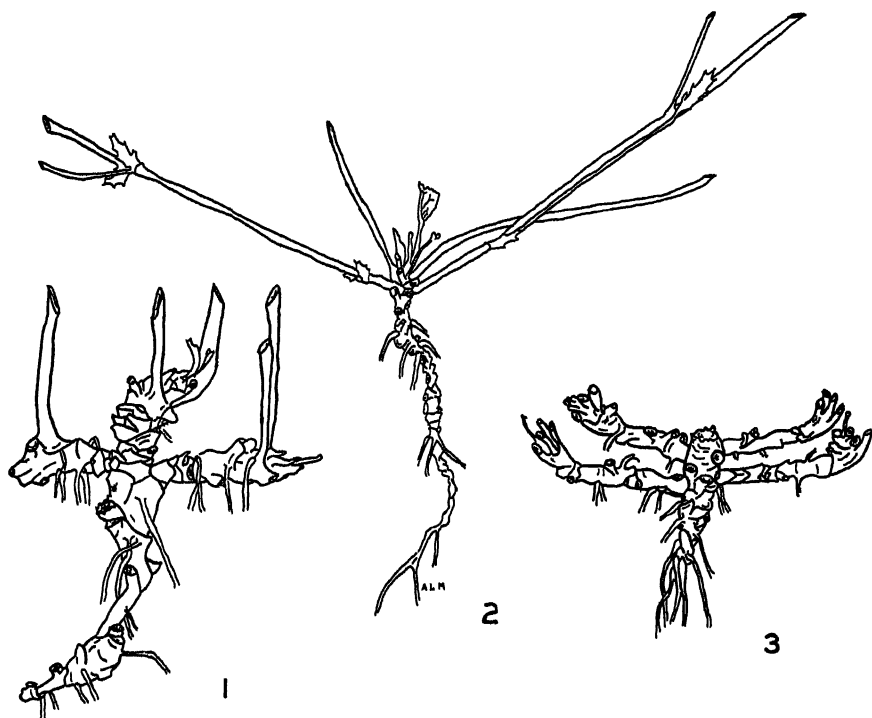
Stem and Leaves. A comparison of the visible characters of the species hybrid and its parents gives evidence that the morphological expression of the hybrid is intermediate, to a greater or lesser degree, depending upon the organ studied, between the morphological expression of each of the parents. Therefore, from a comprehensive study of the hybrid organism, it seems clear that one parent is no more potent than the other in expressing its morphological tendencies in the hybrid. From data presented here, there is no suggestion that the parents express themselves in the hybrid as a mosaic, but rather, it is evident that the hybrid is a compromise expression.

V. conspersa- *Section Nominium Ging.*, *Group Rosulantes Borb.*:¹ this is

¹ A detailed discussion of the growth habits and affinities of the parent species is presented by Gershoy (1934).

a more or less erect blue violet with a slender, woody, indeterminate, orthotropic primary axis (see text fig. 2). Each year in the axils of the leaves are produced aerial leafy branches on which the flowers are borne; these branches usually die back to the base in the fall, although the basal portions may become persistent.

In the early summer and throughout the period of active growth, the cells of the cortex and pith of the determinate axis contain numerous



Figs. 1, 2, & 3. Diagrammatic sketches showing growth habits and relative sizes. Fig. 1. *Viola papilionacea*. Fig. 2. *V. conspersa*. Fig. 3. *V. conspersa* \times *V. papilionacea*. Each figure 2/3 natural size.

plastids and store some starch. In the late summer and autumn these starch grains are hydrolyzed and possibly transported into the perennial stem. In section, the stretched and torn pith and cortical cells of the determinate axis show no starch. In the perennial axis, starch is found in the plastids of the cells of the pith and the cortex in the form of minute, compound grains.

The leaves borne on the acrial stem are comparatively small, and as a rule they are somewhat smaller than those shown in Plate 1, figs. 3a and

3b, which are formed earlier in the spring on the indeterminate axis. The characteristic form expression is that of an ovate blade with an acute apex. The margin is crenate and there is a moderately deep sinus. Blade size is variable depending upon the position (height) of the leaf on the shoot.

V. papilionacea- Section *Nominium* Ging., Group *Boreali-Americanae* Bckr.: the species of this group possess, characteristically, a fleshy, rhizomatous stem as a species character, and are perennials. The orthotropic axis (text fig. 1) in its stretching and elongation tends to become inclined. The lateral axes tend to curve and maintain a certain level at or beneath

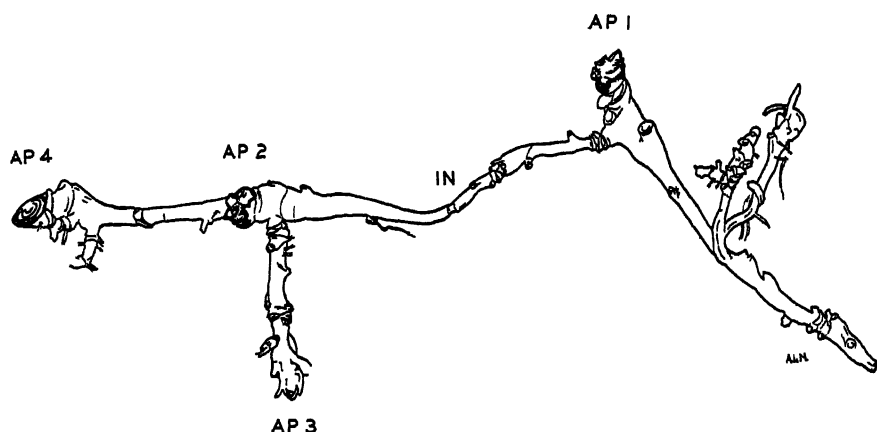


Fig. 4. A semi-diagrammatic sketch of the rhizome of *Viola papilionacea* illustrating the habit of growth and the relation of the lateral shoots to the main shoot. 2/5 natural size.

the surface of the soil. Undoubtedly, several factors control the curvatures. Text figure 4 illustrates the habit of growth and the relation of the lateral shoots to the main shoot. From below the terminal bud (*ap.* 1) of a primary axis arise one or more lateral, monopodial branches quite like the main axis. The growth of these branches is continued into the second season; at the end of the second season of growth, the terminal bud is usually not produced (*ap.* 2) and thus the growth of the perennial plant is continued by the lateral axes (*ap.* 3 and *ap.* 4). The proximal internodes (*in.*) may decay, thus setting free the individuals of a clone, as has been stated by Gershoy (1934). The individuals, aptly called "ramets" by Stout (1929), rapidly form swards in a suitable environment.

The leaves of *V. papilionacea* as compared with those of *V. conspersa* are relatively large. The blade, somewhat variable in shape and size, is

ovate-cordate with an acute apex, and at the base of the blade there is a deep sinus. (See Plate 1, figs. 1a and 1b, for leaf prints.)

Under favorable growth conditions, the hybrid, *V. conspersa* \times *V. papilionacea*, produces a fleshy, orthotropic primary axis (text fig. 3). From this numerous lateral, rhizomatous shoots are produced; these plagiotropic axes extend on or near the surface of the soil. Morphologically, the hybrid stem is intermediate (text fig. 5). The internodes are appre-



Fig. 5. This figure represents comparable figures, obtained from stained sections, of the stem axes of the two species and of the hybrid; *a* is a rhizome of *Viola papilionacea*, *b* is the rhizomatous axis of *V. conspersa* \times *V. papilionacea*, and *c* & *d* are respectively the indeterminate and determinate axes of *V. conspersa*. Somewhat less than natural size.

ciably elongated. However, their length, although it approaches, does not equal that of the internodes of *V. papilionacea*. There are no aerial determinate axes such as are found in *V. conspersa*; the lateral axes of the hybrid are perennial or at least biennial.

Leaf size in the hybrid is variable. Usually, however, the hybrid leaves are larger than those of the seed parent and smaller than those of *V. papilionacea*. The hybrid leaf is also intermediate in character with regard to the depth of the sinus and the serration of the leaf margin. Plate 1

presents comparable figures, from the parents and the hybrid, of leaf form, size, venation, and the character of marginal serration.

CELL SIZE IN THE STEM AND THE LEAF

Cortical Cells in the Stem

The frequency polygons in text figure 6 show the distribution of the cortical cell sizes taken from longitudinal stem sections of *V. conspersa*,

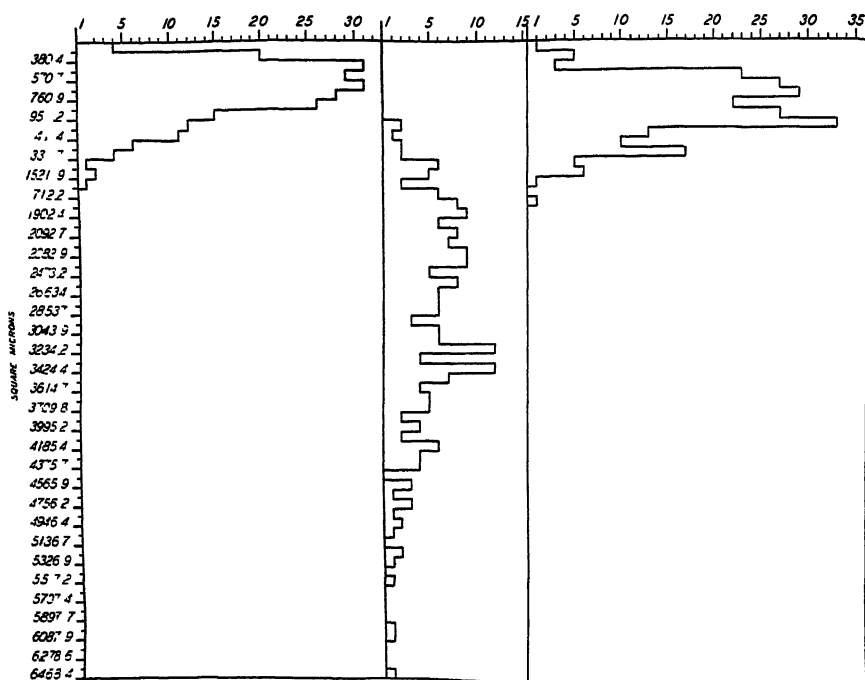


Fig. 6. Frequency polygons showing the distribution of the cortical cell sizes taken from longitudinal stem sections of *Viola conspersa*, *V. papilionacea*, and *V. conspersa* \times *V. papilionacea*.

V. papilionacea, and the hybrid. The cells of *V. conspersa* show a narrow range of size, a definite modal class, and are the smallest in size. In *V. papilionacea* there is indicated a very wide range of cell size, a doubtful modal class, and the presence of much larger cells. In the hybrid the cell size is intermediate, the range in size distribution is narrow, and there is a definite modal class.

Since the cells of *V. papilionacea* show no well defined modal class, a weighted mean was computed for the curves. To obtain this weighted mean, the summation of the product of each frequency and its area was

divided by the total number of individuals. It is thought that this statistically determined weighted mean may be more indicative of a specific cell size characteristic of the tissue than is the modal class. Table 1 correlates roughly the size of the cortical cells with the size of the stem in the species and in the hybrid. In all three cases the cell size is represented by the computed weighted mean of two hundred cells in each case. Organ size is measured by the cross section area of the stem, and the relative sizes are presented as related to the largest size—namely, *V. papilionacea*, which is taken as 100.

TABLE 1

	CELL SIZE, SURFACE AREA (WEIGHTED MEAN) IN SQUARE MICRONS	ORGAN SIZE
<i>V. conspersa</i>	675.0	14
<i>V. papilionacea</i>	2784.0	100
Hybrid	873.0	40

There appears here, in a comparison of cortical cells from comparable organs of related species, a correlation between cell and organ size. The large organ has the larger cells, the small organ has the smaller cells, while in the hybrid, the size of the organ is intermediate, as is also the size of the cortical cells. Sinnott has shown that there is a correlation between cell and organ size in the pith cells of the petioles of *Acer saccharum*, and that in different petioles from the same tree, an increase in organ size is accompanied by an increase in cell size. Amelung, as noted, has shown that there is no correlation between cell and organ size for different leaves from the same plant individual, and for different genera in the same family—for example, he found that the palisade parenchymal cells in the large leaf of *Rheum officinale* were not at all proportionately larger than those from a related plant (*Polygonum cuspidatum*), though in a different genus, bearing small leaves. Cell size tends to be a constant, independent of organ size within the family limits. The size of the organ, according to Amelung, involves not primarily the size but the number of the cells. In the present case, for example, the cortical cells of *V. conspersa* are 24.2% as large as the cortical cells of *V. papilionacea*, whereas the organ is only 14% as large. In the hybrid the cells are 31.4% as large as they are in *V. papilionacea*, whereas the organ is 40% as large. The relative constancy of cell size and its independence of organ size is thus shown to hold true in hybridization.

Census growth, meresis, occurs in meristematic cells that are physiologically young—namely, cells with large nuclei, small vacuoles, and containing a large amount of stored food. Such cells are found in stem apices

and young root tips. Young (1933) has determined quantitatively the limits of the regions in corn root tips where cell division and cell elongation respectively predominate for the various tissues. The cells of the most specialized tissues early cease to divide and continue to grow by elongation only. In the cells of the pith, cell division accompanies elongation and this tissue shows individuality in this persistence of physiological youth. For each tissue, however, the specificity of its cell size in independence of the tissue mass is apparent.

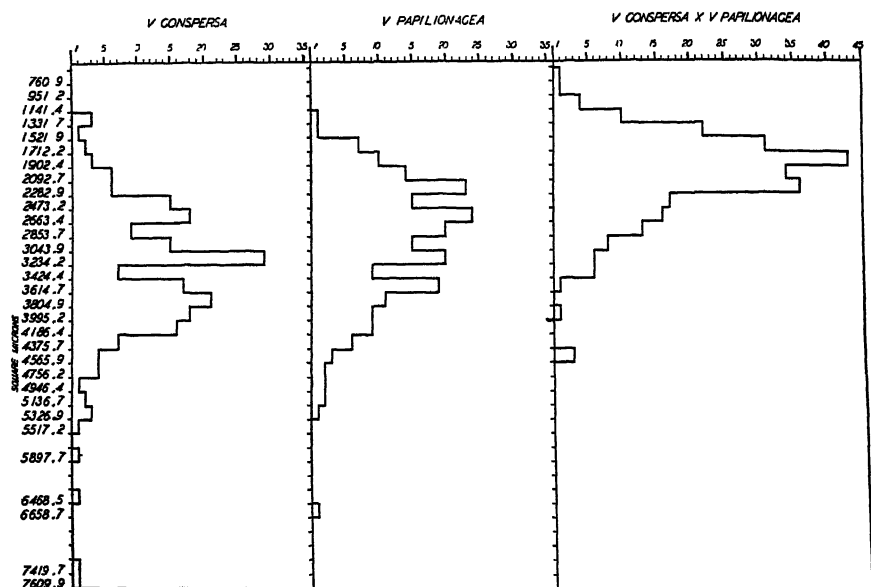


Fig. 7. Frequency polygons showing the distribution of the epidermal cell sizes taken from surface areas of upper epidermal cells of *Viola conspersa*, *V. papilionacea*, and *V. conspersa* \times *V. papilionacea*.

The cortical cells of the perennial axis of *V. conspersa* show little anatomical differentiation. However, they early cease to divide and subsequently grow by elongation. This volume increase of the individual cells is quite independent of the shoot; it is primarily determined by the number of cell divisions (meresis).

The aerial determinate axes of *V. conspersa* show a marked elongation of the internode. The epidermal and cortical cells are elongated to several times their width parallel to the long axis of the organ. These cells contain large vacuoles and very little stored food. Mass growth, auxesis, continues so that some of the pith cells are actually torn. In this connection, Lutman's paper on senescence and rejuvenescence in the potato tuber

(1925) is of interest. He found that cells of the potato tuber were incapable of division when they lacked certain stored foods.

The production of the fleshy rhizome of *V. papilionacea* involves a well marked prolongation of cell division, which is accompanied also by a considerable range with respect to mass growth and the size of the cortical cells. These cells appear to contain a considerable amount of stored food, and they have small vacuoles. In a normal relationship between census growth and mass growth, the former precedes the latter. The demarcation between these two is in some cases very sharp as Young has shown. However, the cortical cells of *V. papilionacea* show considerable persistence in their physiological youth since both census and mass growth continue to occur rhythmically.

Epidermal Cells in the Leaf

The data obtained from measurements of epidermal cells are presented in text figure 7. The range in cell sizes in the two curves representing the two parent species is practically identical. Although there is no well defined modal class, in each curve the distributions are not the same. The curves do indicate, however, that *V. conspersa* has a greater average cell size than does *V. papilionacea*. In the hybrid the range is less extensive as compared with the parents; in addition, the hybrid has a smaller average cell size. In Table 2 a comparison of cell and organ size is made. In all three cases, the cell size for the two hundred cells measured is represented by the computed weighted mean. Organ size is represented in terms of relative blade areas; that of *V. papilionacea*, being the largest, is represented as 100.

TABLE 2

	CELL SIZE, SURFACE AREA (WEIGHTED MEAN) IN SQUARE MICRONS	ORGAN SIZE
<i>V. conspersa</i>	3242.6	16
<i>V. papilionacea</i>	3033.5	100
Hybrid	2070.8	45

It is apparent that *V. conspersa*, possessing the smallest leaves, has epidermal cells of the largest average size. The hybrid, with leaves of intermediate size, has cells of the smallest average size. *V. papilionacea*, producing the largest leaves, has cells that are intermediate in size. It seems evident here that, when parents and hybrid offspring are compared regarding cell size and organ size, there is no correlation between the size of the epidermal cells and the size of the leaf. Amelung found, in comparing organs of different size on the same plant individual, that differences in

organ size were not accompanied by differences in the size of the epidermal cells. Thus epidermal cell size was not correlated with organ size differences on the same individual. However, in his comparison of two genera with very widely different leaf sizes, *Rheum officinale* and *Polygonum cuspidatum*, he found in the cells of the palisade parenchyma a correlation between cell and organ size. This correlation was, however, by no means so marked as that between cell sizes from different sized organs but from the same individual.

Starch Grains

No attempt was made to plot the relative sizes of the starch grains. It appeared, however, from a careful examination of numerous cells, that the starch grains in the hybrid are intermediate in size between the small grains of *V. conspersa* and the large grains of *V. papilionacea*. In addition, it was observed that the grains of *V. conspersa* are several to many times compounded, while the grains of *V. papilionacea* are solitary, double, and rarely several times compounded. In the hybrid the degree of compounding seems to be intermediate.

DISCUSSION

The Leaf

It seems apparent, as shown in the photographs (Plate 1), that the size and form of the leaves in the hybrid manifests some degree of intermediate inheritance. From a study of the leaf prints, it seems clear that, in the shape of the leaf and in the character of the marginal serrations, the hybrid leaf is an intermediate, compromise expression. A study of the leaf blade areas of comparable leaves from the hybrid and its parents shows the hybrid organ to be intermediate in size. From these data, it appears that, in the size and shape of the leaf, the parents were equally potent in the degree to which their morphology was expressed in the hybrid.

The data from the measurements of epidermal cells as presented in text figure 7 show the distribution of cell sizes for the two parents to be nearly the same, with no well defined modal classes. The weighted means show the epidermal cells to be only slightly different in size although the organ size in one case is more than six times greater than the organ of the other parent. Tenopyr, however, has shown, in a comparison of the epidermal cells from the leaves of the common and the Witloof chicory, that there is a difference in the size of the epidermal cells, the leaves of the Witloof variety having larger cells than the leaves of the wild variety. Amelung and Sinnott have shown that epidermal cell size is not correlated with differences in organ size on the same individual. My data indicate

that the differences in size between the leaves of these two species is due to the number of cells rather than to the size of the cells, or to the combined effect of the size and the number of the cells. The hybrid leaf attains a size that is intermediate between the parent organs, and it is composed of cells considerably smaller than those found in the epidermis of the leaves of either parent.

The Stem

From the drawings of the stems of *V. conspersa*, *V. papilionacea*, and the hybrid, it seems apparent that the hybrid stem, while more thick and fleshy than the slender, woody stem of *V. conspersa*, is not equal in thickness to the stem of *V. papilionacea*. The perennial axes of the hybrid in which internode elongation has occurred have an internode length which approaches that found in the perennial axes of *V. papilionacea* and which is much longer than the internode length of *V. conspersa*. The thick, fleshy stem and lateral axes of the hybrid are strongly suggestive of the rhizomes of *V. papilionacea*. The perennial lateral axes are plagiotropic as are the lateral axes of *V. papilionacea*; the apices turn up, however, as if to become orthotropic. Some of the flowering aerial axes of *V. conspersa* may fail to attain their full growth in one season, and they persist into the following season. The internodes of such branches are short and the appearance of such partially condensed axes, oriented in a more or less transverse, geotropic position, resembles the elongated, rhizomatous axes of the hybrid. The axes of *V. papilionacea* contain much stored starch: the cells seem more densely crowded with starch grains than do the cells of *V. conspersa*.

For the material studied, the data indicate a representative cortical cell size for each parent and for the hybrid, that of the hybrid being intermediate between those of the parents. The works of Amelung, Sierp, Tenopyr, Sinnott, Lutman, and others show the difficulties which arise in an attempt to determine a specific cell size for a species. Thus the sizes determined as characteristic for the tissues studied here are not to be considered as specific cell sizes. However, for these data, it appears that, for comparable tissues from comparable regions, there is a representative cell size particular for the tissue, and this may be used in comparing cell and organ sizes.

According to the data presented herein, in comparing cortical cell sizes from stems of individual plants of related but not the same species, there is a correlation between cell and organ size. The large organ has cells which are larger than those of the small organ. This is in accord with Amelung's results where he compared palisade parenchymal cells from

comparable organs on two individuals of different genera but the same family. The hybrid organ is intermediate in size and the same is true for the size of its cortical cells.

From these data on the leaf and the stem, two observations are clear: 1) In both cases organ size is intermediate in the hybrid. 2) Cell size, however, may or may not be correlated with organ size when species are compared, depending upon the tissue studied.

That in some tissues of the hybrid the cells are intermediate in size, and that in others the cell size is smaller than in either or both of the parents is quite significant. The theoretical implications suggested are that the cell size is in part at least a function of the intercellular relations in an organ. These relations are influenced by the physiological-anatomical character of the organ, and in turn by the well known influence of functional factors on the intimate character of the cell. Environmental factors in their turn affect cell size. A discussion of these inter-relationships has been presented by Amelung (1893), and recently by Sinnott (1930), and Gershoy (1934). On the other hand, in organ size, in all cases studied, there is an intermediate expression of the parental characters. This expression seems to be influenced only secondarily by the functional and physiological factors affecting cell size, since cell size in these cases plays only a small part in the achievement of organ size. Organ size depends upon the number of cell divisions, a phenomenon which seems to be determined early in the ontogeny of the organ.

SUMMARY

A species hybrid, *Viola conspersa* × *V. papilionacea*, and its parents were compared in order to determine especially the cell size and organ size relationships in the leaf epidermis and the cortex of the stem.

1. In a comparison of epidermal cell size and organ size, there is no correlation, since, despite a wide range in organ size, epidermal cell size is relatively constant.

2. Cortical cell size and organ size were compared in the species hybrid and its parents. There is a correlation between cell and organ size: the largest cells are found in the larger organ.

3. From these data there seems to be a relatively constant cell size for the tissue studied. The hybrid cell size is different from that of either parent and, depending upon the tissue studied, may or may not be intermediate between the parental cell sizes.

4. In the two organs studied, the size of the hybrid organ is intermediate between the sizes of the parent organs.

5. From the frequency polygons of the epidermal and cortical cell

sizes, there is no suggestion that the range of cell size in the hybrid presents a mosaic pattern.

I am deeply indebted to Dr. A. Gershoy for the use of his material and for his stimulating criticism and advice. It is with considerable pleasure that I acknowledge the kind interest and many helpful suggestions of Professors R. A. Harper, G. P. Burns, and B. F. Lutman. The drawings, carefully prepared by Alice L. Marvin are gratefully acknowledged.

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Explanation of Plate 1

(all figures reduced to 4/5 natural size)

Fig. 1a. Mature basal leaf of *V. papilionacea*.

Fig. 1b. Mature leaf of *V. papilionacea*. This leaf was formed later than 1a.

Fig. 2a. Mature basal leaf of *V. conspersa* \times *V. papilionacea*.

Fig. 2b. Mature leaf of *V. conspersa* \times *V. papilionacea* formed later than 2a.

Fig. 3a. Mature basal leaf of *V. conspersa* borne on the indeterminate axis.

Fig. 3b. Mature leaf of *V. conspersa* borne on the indeterminate axis but formed later than 3a.



MARVIN TWO VIOLET SPECIES

A new *Houstonia* in southcentral Texas

C. H. MUELLER AND MARY T. MUELLER

During February and March, 1934¹ an apparently undescribed species of *Houstonia* was collected by the authors in various parts of Dewitt and Victoria Counties, Texas. It is found commonly scattered on the deep sandy prairie in open savannas of *Quercus marylandica* and *Q. stellata*.

The plant's annual habit and singly disposed flowers on erect peduncles which are never reflexed in fruit distinguish it from all other known species in our range except *H. minima* Beck., *H. parviflora* Holzinger, and *H. pusilla* Schoepf. [*H. minor* (Michx.) Britton]. From *H. minima* and *H. parviflora* it is distinguished by its corolla tube which much exceeds the calyx lobes. It differs from *H. pusilla* (with which it has frequently been confused) in having a light pink or lavender corolla yellow centered and hairy within the throat as well as more flat fruits and narrower leaves.

Houstonia pygmaea C. H. & M. T. Mueller sp. nov.

Annual; stems simple in young plants with the leaves forming a basal rosette, in older plants much branched at the base and subsequently forked, 1-2 cm. and finally 3 or 4 cm. long, procumbent or sometimes erect, forming a somewhat dense tuft except in shade forms which are slender; leaves finally distributed, the lower ones lanceolate to spatulate, the blades about 2×4-8 mm., acute, gradually tapering at the base into a petiole 2 or sometimes as much as 7 mm. long, the upper ones linear-lanceolate to broadly oblanceolate, short-petiolate or sessile, the blades about 1-2×4-6 mm., all blades and the wing-like edges of the petioles sparsely ciliate with short, thick hairs; stipules white, roughly ciliate, little more than a line between the leaf bases; peduncles erect, never horizontally disposed and never reflexed at maturity, slender, about 2.5-5 mm. long, accrescent; calyx lobes narrowly lanceolate, about 2 mm. long at flowering, sometimes becoming 3-4 mm. long and more broadly lanceolate in fruit; corolla infrequently persistent until the calyx lobes almost equal the tube, loosely salverform (hardly funnel-shaped), pink or lavender or sometimes almost white, the tube about 5 mm. long or a little less, much surpassing the calyx, the throat densely short, white hairy within, the limb about 6-9 mm. across, divided almost to the yellow throat into ovate, acute lobes 3-3.5 mm. (or rarely only 2 mm.) long and about 1.5-2.5 mm. broad; stamens inserted well above the middle of the corolla tube; style about 1 mm. long; stigmas narrowly oblong, densely short hairy, not spreading; fruit about two-thirds included in the hypanthium which reaches about 1.5 mm. in height, capsule didymous, very flat, about 2-2.5 mm. high, 3-4 mm. broad, and 1 mm. thick; seeds about 5-20 in each cell, minutely pitted and concave

¹ A very mild winter had permitted spring annuals to mature about a month early.

on the placental side, as large as $0.2 \times 0.3 \times 0.6$ mm. when only five in a cell, but variously reduced in size when more numerous.

Annua, caules simplices vel ramosi, procumbentes vel erecti; folia ex lineari-lanceolatis late spathulata, inferiora petiolata, superiora sessilia, sparse ciliata, laminis 4–6 mm. longis 1–2 mm. latis; stipulae albae deciduae; pedunculi circiter 2–8 mm. longi erecti maturitate non reflexi; calycis lobi anguste lanceolati circiter 2 mm. longi accrescentes; corolla hypocrateriformis vel late infundibulariformis rosea vel pallide purpurea, tubo circiter 5 mm. longo calycem multo superante, limbo 6–9 m. lato centro flavo, fauce intus pubescente; fructus tertia parta ex hypanthio exsertus; capsula complanata 2–2.5 mm. alta, 3–4 mm. lata, 1 mm. crassa; semina in quoque loculo circiter 5–20.

Type specimens (Mueller nos. 3 and 4) collected February 16 and March 6, 1934 in Dewitt Co., Texas are deposited in the herbarium of the authors at Cuero, Texas. Co-types are preserved in the herbarium of the New York Botanical Garden.

CUERO, TEXAS

Additions to the genus *Amsonia*

ROBERT E. WOODSON, JR.

Since the appearance of the writer's monograph of *Amsonia* in 1928,¹ five additional species have been proposed from time to time extending both our knowledge of the biological entities of the genus and the synonymy concerned with pre-existing species. Shortly after the completion of the monograph, increased information regarding certain plants of the Ozark Plateau and adjacent territory to the southwest necessitated the recognition of *A. illustris* Woods.² as distinct from *A. Tabernaemontana* Walt. In 1931³ two more species were reported from Arizona and Chihuahua respectively: *A. arizonica* A. Nels. and *A. filiformis* A. Nels. The former has subsequently been found to be conspecific with *A. pogonosepala* Woods., while the type collection of the latter (C. G. Pringle 6796) is likewise the type of *A. arenaria* Standl. More recently⁴ two additional species have been reported from the Southwest, *A. grandiflora* Alexander and *A. lanata* Alexander, differing from *A. longiflora* Torr. and *A. tomentosa* Torr., respectively in little else than slight discrepancies in the dimensions of the corolla. It is obvious that in such ambiguous entities additional specimens augmented by field observation are greatly needed as aids to taxonomic interpretation. The same need is manifest with regard to the following "herbarium species" which appear to merit recognition:

Amsonia Peeblesii Woodson, spec. nov. Herbacea perennis plus minusve erecta 5–6 dm. alta; ramis ramulisque gracilibus glaberrimis; foliis alternatis rariusve approximatis lineariellipticis apice obtuse acuminatis basi attenuatis 7–10 cm. longis 0.2–0.4 cm. latis superne minoribus glaberrimis subsessilibus; inflorescentiis irregulariter cymosis laxe plurivel paucifloris longiuscule pedunculatis (foliis valde superantibus); pedicellis 0.2–0.3 cm. longis post maturitatem paulo accrescentibus glabris; bracteis inconspicuis angustatis 0.1–0.2 cm. longis subfoliaceis; calycis laciniis linearibus obtuse acuminatis 0.6–0.65 cm. longis 0.05–0.07 cm. latis glabris vel apicem versus sparse pilosulo-barbellatis subfoliaceis; corollae tubo 1.7–1.8 cm. longo basi ca. 0.1 cm. diametro metiente prope insertionem staminum paulo ampliato deinde paululo angustato faucibus ca. 0.2 cm. diametro metientibus pallide livideque caeruleo prope basem etiam saturate extus glabro intus villosulo lobis oblique elliptico-ovatis obtusis 1.0–1.2 cm. longis patulis pallidissime caeruleis fere albidis; antheris 0.2 cm. longis paulo supra medio corollae tubi insertis; ovariis ovoideis ca. 0.15 cm. longis glaberrimis; stigmatibus capitato-maniculato apice

¹ Woodson, R. E., Jr. 1928. Ann. Mo. Bot. Gard. 15: 379–434.

² Woodson, R. E., Jr. 1929. Loc. cit. 16: 407.

³ Nelson, A. 1931. Amer. Journ. Bot. 18: 432; 433.

⁴ Alexander, E. J. 1934. Torreya 34: 116; 117.

obtuse bilobato; folliculis immaturis 10–12 cm. longis haud articulatis glaberrimis; seminibus ignotis.

ARIZONA: near Leupp, Coconino Co., May 27, 1934, *T. H. Kearney and R. H. Peebles 9568* (Herb. Missouri Bot. Garden, TYPE).

Mr. Peebles has added the following note concerning the affinities of this plant: "This plant belongs to subgenus *Sphinctosiphon*, having the stigma surmounted by two distinct lobes, and pods not constricted. It seems nearest *A. Palmeri* Gray, but the corolla lobes are 12 mm. long; calyx lobes are glabrous (rarely a single hair on margin)." The corolla tube is also decidedly longer in *A. Peeblesii* than in *A. Palmeri*, and the insertion of the stamens is somewhat lower within the corolla tube of the former, with a correspondent difference in the general shape of the throat. The same species has recently been collected by Mrs. McKelvie in the vicinity of Cameron, some distance down the Little Colorado River from Leupp.

Amsonia glaberrima Woodson, spec. nov. Herbacea perennis plus minusve erecta 6–7 dm. alta; ramis ramulisque glaberrimis gracilibus; foliis oblongo-ellipticis acute acuminatis 5–7 cm. longis 1.5–2.4 cm. latis glaberrimis firme membranaceis supra paululo lucescentibus subtus opacis; petiolis 0.2–0.4 cm. longis; inflorescentiis irregulariter cymosis aggregatis paucivel plurifloris breviuscule pedunculatis (foliis haud superantibus); pedicellis 0.3–0.35 cm. longis post maturitatem paulo accrescentibus glabris; bracteis inconspicuis linearibus vix 0.1 cm. aequantibus; calycis laciniis ovato-trigonalibus acutis 0.15 cm. longis glaberrimis; corollae tubo 0.65–0.7 cm. longo basi ca. 0.1 cm. diametro metiente deinde gradatim ampliato faucibus ca. 0.2 cm. diametro metientibus delicate caeruleo prope basem paululo fuscente extus omnino glaberrimo intus prope insertionem staminum villosulo lobis oblique ovatis obtusis 0.6–0.7 cm. longis dilute caeruleis glabris patulis; antheris ca. 0.1 cm. longis prope corollae fauces insertis; ovariis ovoideis ca. 0.1 cm. longis glabris; stigmatibus capitato-maniculato haud manifeste apiculato; folliculis immaturis gracillimis falcatis haud articulatis glaberrimis; seminibus ignotis.

LOUISIANA: low prairies, Welsh, Jeff Davis Parish, May 17, 1915, *E. J. Palmer 7660* (Herb. Missouri Bot. Garden, TYPE).

This plant appears to combine certain aspects of both *A. Tabernaemontana* and *A. ciliata*. The corolla is totally glabrous without, as in the latter species, while the leaves assume the size and shape of the former, although somewhat smaller than those of any specimens of it which are available for my observation in the herbarium collections of the Missouri Botanical Garden.

MISSOURI BOTANICAL GARDEN

WASHINGTON UNIVERSITY (St. Louis)

Overwintering of *Synchytrium decipiens* in New York

J. S. KARLING

One of the many puzzling problems in relation to *Synchytrium decipiens* Far. is the manner in which this chytrid hibernates through the winter. Unlike the majority of species of this genus, it never forms, as far as is known, thick-walled resting sporangia to carry it over unfavorable seasons, but only summer sori and evanescent zoosporangia, which quickly collapse and die when exposed to the air. Furthermore, its host, *Falcata comosa* (*Amphicarpaea monoica*) is an annual which dies and dries up with the onset of cold weather and frost and does not reappear again until fairly late in the following spring. Yet in spite of these handicaps *S. decipiens*, when once established in a community of wild peanuts, almost invariably reappears on the host seedlings in the spring from year to year. The author's attention was first directed to the persistence of this parasite in 1931 while collecting material for cytological study of nuclear division, and careful observations were immediately begun in Van Cortlandt Park in New York City to record the appearance of the fungus as well as its method of hibernation. The upper part of this park is quite wild, shady and swampy, and the soil is continually damp and mucky, affording thus an exceptional environment for a luxuriant growth of the hog peanut.

In the course of these observations it was noted that in late September and early October deep seated, dark and shiny sori were formed on the stem, and in view of the fact that these did not dehisce at once when mature like the earlier orange colored ones it was assumed that they were dormant sori which remained alive during the winter and served thus to infect the host seedlings in the following spring. On this assumption seeds of *Falcata comosa* were collected and sown in the greenhouses at Columbia University during November of 1931, and the seed beds were then covered with a mat of heavily infected, dead stems and leaves of the host plant. When the seeds began to germinate in approximately three weeks, the beds with their covering were wetted thoroughly every day. As the seedlings emerged they were thus forced to grow and push through the wet covering of decayed and infected peanut stems and leaves, and ample opportunity was thereby afforded for infection in case the chytrid zoosporangia were still viable. Additional supplies of infected dried stems were brought in from time to time, and the experiment was duplicated during the successive winter months of that year to allow for the possibility that the fall sporangia of *S. decipiens* might require alternate thawing and freezing as well as a rest period for successful infection. The results for the winter of 1931-32 were all negative, and in the following winter the experiment was

again replicated without positive results. Out-of-doors, however, infection occurred in abundance during the spring as the host seedlings emerged from the ground. In 1932 the hog peanut seedlings emerged from the ground on April 29, but no infection was visible until May 10, when the plants were approximately two and a half inches tall. In 1933 abundant infection was found on May 14, and in the following year it was not until May 20 that any infection could be observed. The winter of that year was unusually cold in New York City with temperatures as low as -14°F. , and traces of snow remained on the ground until late in March. In 1935 the winter was considerably milder, with the result that germinating underground fruits were found in abundance on April 15. However, no infection was found until May 25, when some of the plants were as much as six inches in height. From these records it seems apparent that infection occurs in the young seedling stage, possibly as they are emerging from the seed coat and ground, but does not become evident until somewhat later as the sori and zoosporangia mature.

It thus seemed obvious that some other means of hibernation than in the dead stems occurred. Attention was therefore directed to the underground fruits which are produced so abundantly by the hog peanut and remain alive in a dormant condition during the winter. It was immediately observed that these peanuts became heavily infected with *S. decipiens*, which develops deep seated and dark colored sori. Apparently infection occurs very early while the fruits are aerial, since infected, elongating flower stalks have frequently been observed. *Falcata comosa* forms both casmogamous and cleistogamous flowers, with the result that two kinds of fruits or seeds are to be found. The former develop into aerial, elongated, many-seeded pods, while in the latter the flower stalk begins to elongate after fertilization and forms usually a single-seeded fruit which grows into the ground, where it lies dormant until the following season. These underground peanuts are thus the only portion of the host plant besides the aerial casmogamous fruits which remain alive during the winter. It is not uncommon to find the pods of the latter also heavily infected with deep seated sori in the fall, but in no instances so far have I observed the parasite penetrating to the seeds themselves. The possibility that *S. decipiens* may be seed-borne is thus rather remote.

The sori which develop on the underground peanuts are strikingly similar in appearance to those formed late in the summer and fall on the stems and pods, and are confined without exception, as far as my observations go, to the thin outer covering of the fruits. No infection of the cotyledons has yet been found. The occurrence of these sori on the dormant underground fruits suggested at once that this was the manner by which

S. decipiens was carried over the winter. Accordingly in November and December of 1933 a large number of infected underground fruits were collected and planted in the greenhouses. Germination occurred within fourteen days, and after twenty-eight days when the seedlings were approximately three inches high 8% were found to be infected. These remained somewhat stunted in growth, but served as sources of infection, so that in a few weeks most of the plants were parasitized. Concurrent with these experiments sporangia from infected fruits were brought into the laboratory and mounted in hanging drops to test their viability. Germination was exceptionally sparse, and in only two instances were motile zoospores formed, indicating that the percentage of viability, in my material at least, is very low. Similar germination tests with infected underground fruits were made during the winter of 1934, and within approximately six weeks 14% of the seedlings showed infection. In these experiments as well as those of the previous year a small amount of soil from the field was allowed to remain on the fruits at the time of planting, which of course did not preclude the possibility that the fungus might have hibernated and been carried over in the adhering soil. With this in mind the peanuts were thoroughly washed before planting in 1935 so that no foreign material except the sori remained on the surface. In this season infection was as high as 18%.

In view of these experimental results and observations extending over a period of several years, it is apparent that, in the vicinity of New York City at least, the late summer and early fall sori and sporangia of *S. decipiens* may remain dormant on the coats of the underground fruits during the winter, and infect the young seedlings in the following spring. In Japan, however, according to Kusano (1932),¹ *S. decipiens* hibernates in the dead and dried vines. Kusano reports that the dark colored, deep seated dormant sori are never developed on the lower and older, but only on the upper portions of the host plant in the fall. Such dormant sori when brought into the laboratory at various intervals during the winter and kept fairly moist dehisced and liberated zoosporangia, which underwent cleavage and formed motile cells in from two hours to several days. The viability of the zoosporangia through the winter was found to depend primarily on moisture relations. Although Kusano succeeded in germinating the zoosporangia, he made no greenhouse tests to determine whether or not seedling infection would occur during the winter.

It is thus obvious that my observations and results on *S. decipiens* in the vicinity of New York City differ in many respects from those of

¹ Kusano, S. 1932. Dormancy in the summer sorus of *Synchytrium*. Jour. Coll. Agric. Imp. Univ. Tokyo 11: 427-439.

Kusano in Japan. In the first place, abundant deep seated sori have been found in late summer and early fall on the lower and older as well as the younger portions of the vines in addition to those on the underground fruits. In many instances such sori have been seen to extend almost to the point where the vines emerge from the ground. Such infection apparently occurs on wet and rainy days as the zoosporangia and zoospores are carried downwards. Secondly, the zoosporangia from undehisced sori on dead and dried vines collected out-of-doors at various intervals during the winter have not only failed to germinate in hanging drops in the laboratory but also to produce infection of emerging seedlings in the greenhouses over a period of several years. In these tests conditions were made as favorable as possible for successful infection, but without positive results. Kusano does not report the occurrence of sori on the underground fruits, but it is probable that they were overlooked as sources of infection in Japan. While *Falcata comosa* is an annual, we have, nevertheless, in these underground fruits host tissues which are comparable, as far as hibernation of a parasite is concerned, to the stems and leaves of perennials. The fact that they occur underground insures in most instances sufficient moisture to keep the fungus alive in case, as Kusano claims, moisture is the dominant factor in viability.

There are thus, according to Kusano's and my observations, two means of hibernation of *S. decipiens* in *Falcata comosa*: (1) by dormant sori and zoosporangia in the dead and dried vines, and (2) on the underground fruits. However, the possibility that occasional resting spores are formed and thus serve as means of hibernation must not be excluded. Although no such structures have yet been observed, our search may not have been sufficiently intensive, and it is not altogether improbable that they may occur occasionally.

COLUMBIA UNIVERSITY
NEW YORK CITY

INDEX TO AMERICAN BOTANICAL LITERATURE 1931-1935

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Miocene plants from Colombia, South America

EDWARD W. BERRY

(WITH PLATES 2 AND 3 AND TWO TEXT-FIGURES)

The plants described in the following notes have been turned over to me from time to time during the last few years by the Tropical Oil Company. They come from three localities on the De Mares concession, which is located in the Magdalena Valley, Department of Santander, Colombia, about 350 miles south of the Caribbean coast.

Relatively little is known regarding the Tertiary floras of Colombia. With the exception of two species of fossil fruits described recently without locality by E. M. Reid,¹ the previous contributions were enumerated by me² in 1929 and need not be repeated in the present connection.

The material is limited in amount and rather poorly preserved and it has been possible to make more or less satisfactory identification of only 17 different forms. These represent 16 genera in 13 families and 11 orders.

All belong to the dicotyledonous angiosperms except 2 species representing 2 families and 2 orders of Monocotyledonae. They are wet tropical forms and obviously do not present any sort of picture of the flora which must have existed in the region at the time they were living. Many families which inhabit the country at the present time and which were undoubtedly present during the latter half of the Tertiary, for example, the Leguminosae, are not represented.

Nor can anything be said about the ecology except that certain of the fossils represent coastal forms, such as the *Avicennia*, and others occur in Tertiary floras of known coastal habit, so that there is some slight evidence that the sea margin was not far distant at the time the plants were preserved. Four species are new, and several others which are too poorly preserved for specific description, appear to represent new forms. Nine species have an outside distribution and three additional are represented in other areas by closely related forms. These facts and the local distribution are shown in the accompanying table.

AGE OF THE DEPOSITS

The fossil plants from the De Mares concession are much too few in number and too indefinite specifically to afford a basis for close correlation, and even if they were more abundant, well preserved and certainly determinable, the question of exact age would still be a problem, since most of the outside localities with which they might be compared are somewhat

¹ Reid, E. M. Rev. Géogr. Phys. & Géol. Dynamique, 6, fasc. 3, 1933.

² Berry, E. W. Proc. U. S. Natl. Mus. 75, art. 24: 1-12, pls. 1-5, 1929.

[THE BULLETIN FOR JANUARY (63: 1-52) WAS ISSUED JANUARY 2, 1936]

uncertain in age due to differences of opinion among the students who have studied the various deposits. ▶ ▶ ▶

One thing at least is certain, i.e., the three stations from which fossil plants have been collected on the concession are at least approximately of the same age, as is shown by the fact that the two species found at Station 19 N., 2 W. are present at both of the other stations, and one of these, *Mespilodaphne colombiana*, is a new species unknown at outside localities; and of the seven species named from Station 35 S., 25 W., all but two are present at one or the other of the other two stations.

	27 N., 2 E.	19 N., 2 W.	35 S., 25 W.	COLOMBIA			VENEZUELA			TRINIDAD S.W.I.		LOJA, ECUADOR	COSTA RICA	TERUANTEPEC, MEXICO	SOMBRITO FORMATION PERU	COLLAZO BEALINE PUERTO RICO
				SANTA ANA	LEIVA	RUGA, CAUCA VALLEY	BETJOQUE	LA VICTORIA	PALMAJERO	SIPARIA	FOREST SAND					
<i>Dioscorea</i> sp.	x						o						o			
<i>Palmophyllum</i> sp.	x		x				o		o							
<i>Ficus talamancana</i>													x	x		
<i>Ficus</i> cf. <i>betijoquensis</i>	x						x									
<i>Coussapoa</i> sp.	x		x				o							o		
<i>Anona</i> cf. <i>guppyi</i>	x		x				x	x								
<i>Tapirira lanceolata</i>	x								x			x			x	
<i>Rheedia miocenica</i>			x							x						
<i>Buettneria</i> sp.	x			o												
<i>Hernandia tongi</i>	x							x								
<i>Persea coriacea</i>			x	x	x											
<i>Mespilodaphne colombiana</i>	x	x	x													
<i>Eugenia comparabilis</i>	x	x	x							x	x					x
<i>Couroupita santanderensis</i>																
<i>Avicennia miocenica</i>	x															
<i>Posoqueria columbiana</i>						x										
<i>Phyllites</i> sp.	x															

x = Identical.

o = Similar.

Another certainty is that the age is Miocene. There can be no doubt of this, but whether Lower, Middle, or Upper remains doubtful. As will be seen in the accompanying table of distribution one species, *Persea coriacea*, is known from beds which seem to be Upper Miocene, but about which no certainty can be expressed. Four come from beds elsewhere which are either Lower or Middle Miocene, three from beds which are Middle or Upper Miocene, and one from beds which are Lower to Upper Miocene. I have also shown in the table outside formations containing plant species most similar to De Mares species. Among these there are

three whose age is Lower or Middle Miocene and one from beds which are Middle or Upper Miocene.

Evaluating this distribution for what it appears to be worth it would seem to me that the De Mares plant bearing outcrops are probably of Middle Miocene age, but I would certainly not be dogmatic in that opinion.

In a preliminary report to the Tropical Oil Company on two specimens from Station 27 N., 2 E., dated July 25, 1930, I stated that although not certain they appeared to be of Upper Miocene age. The larger collections received after that date render the question of age more instead of less confusing. It is possible that the age may be Upper Miocene.

Order LILIALES
Family DIOSCOREACEAE
Genus DIOSCOREA Linné
Dioscorea sp.
Text-figure 1

Leaves of large size, presumably cordate, with entire margins, stout petiole and palmately 7 to 9 veined from the top of the petiole. Secondaries mostly transverse. The single specimen, preserved in a coarse matrix, is very vague away from and between the primary veins and it is not possible to frame a satisfactory diagnosis. In many ways it suggests comparisons with the somewhat smaller leaves from the Miocene of southern Costa Rica which were described as *Piperites cordatus*³ and which also appear to be present at Betijoque, Venezuela, and in the Forest Sand of Trinidad, B. W. I. Probably none of these are specifically identical with one another. The genus has not before been found fossil, but the family is represented by the genus *Dioscorites* Saporta from the Upper Cretaceous to the Oligocene, and possibly by the genus *Majanthemophyllum* O. Weber with numerous species from the Mid-Cretaceous to the Lower Miocene. *Dioscorea* has over 200 existing species, cosmopolitan in warm climates and sometimes extending long distances into the Temperate zone.

Occurrence: 27 N., 2 E.

Order ARECALES
Family ARECACEAE
Genus PALMOPHYLLUM Conwentz
Palmophyllum sp.

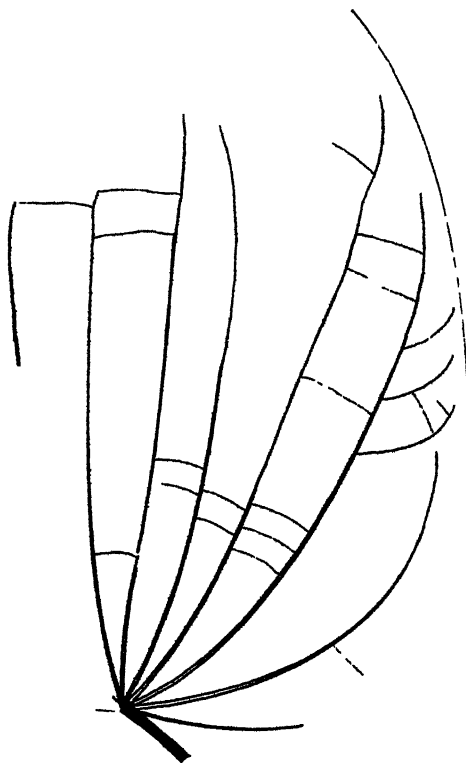
Fragments of palm rays are referred to the genus *Palmophyllum* as a form genus. They may be the same as what was called *Sabalites* sp.⁴ from Betijoque, State of Trujillo, Venezuela. They are too inconclusive to be of either geo-

³ Berry, E. W. Proc. U. S. Natl. Mus. 59: 171, pl. 22, fig. 1, 1921.

⁴ Berry, E. W. Proc. U. S. Natl. Mus. 59: 562, pl. 109, fig. 3, 1921.

logical or botanical interest beyond indicating the presence of palms in this fossil flora.

Occurrence: 27 N., 2 E. and 35 S., 25 W.



Text-figure 1

Dioscorea sp.

Order URTICALES
Family MORACEAE
Genus *FICUS* Linné
Ficus talamancana Berry
Plate 2, Figure 1

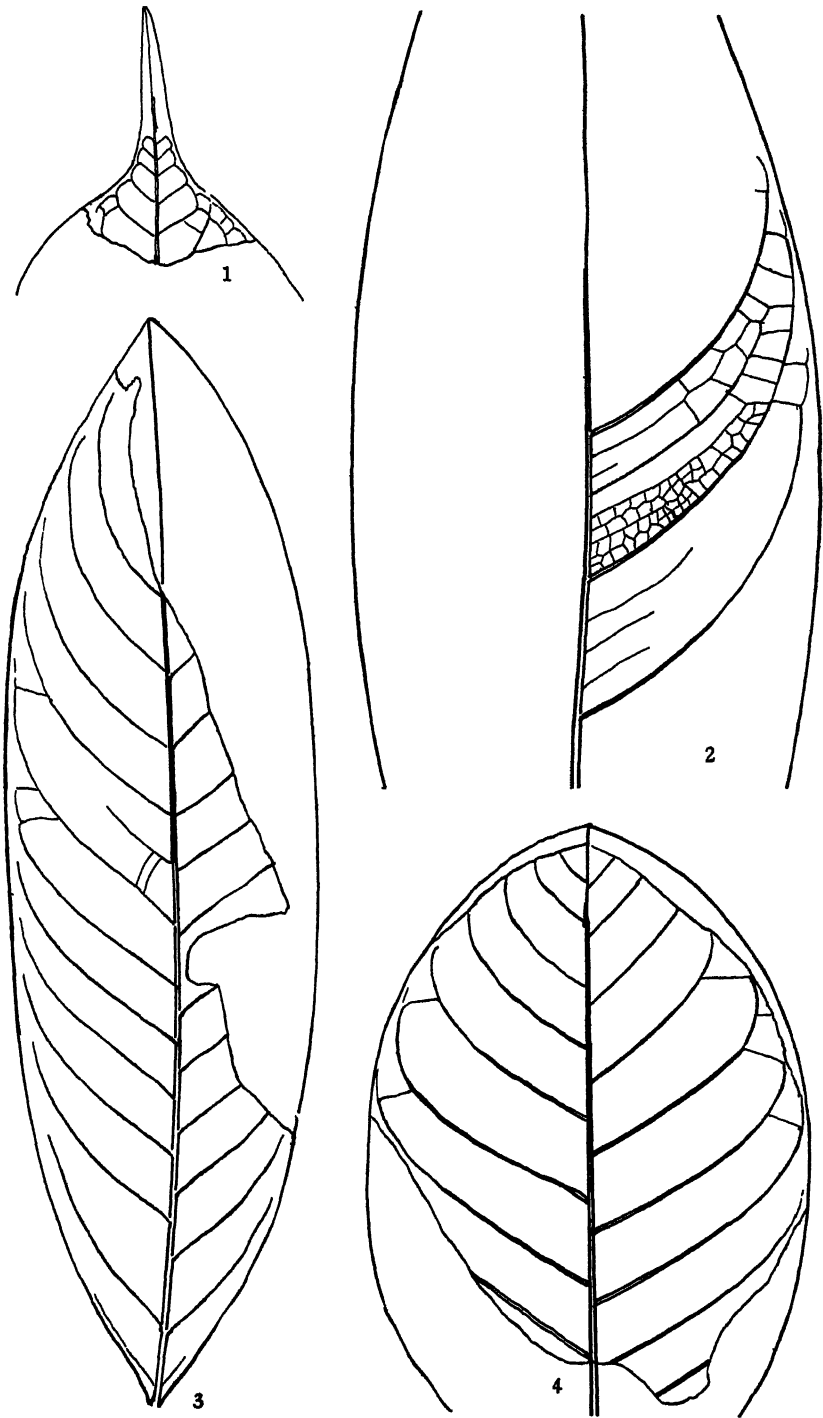
Ficus talamancana Berry, U. S. Natl. Mus. Proc. 59: 172, pl. 23, 1921.

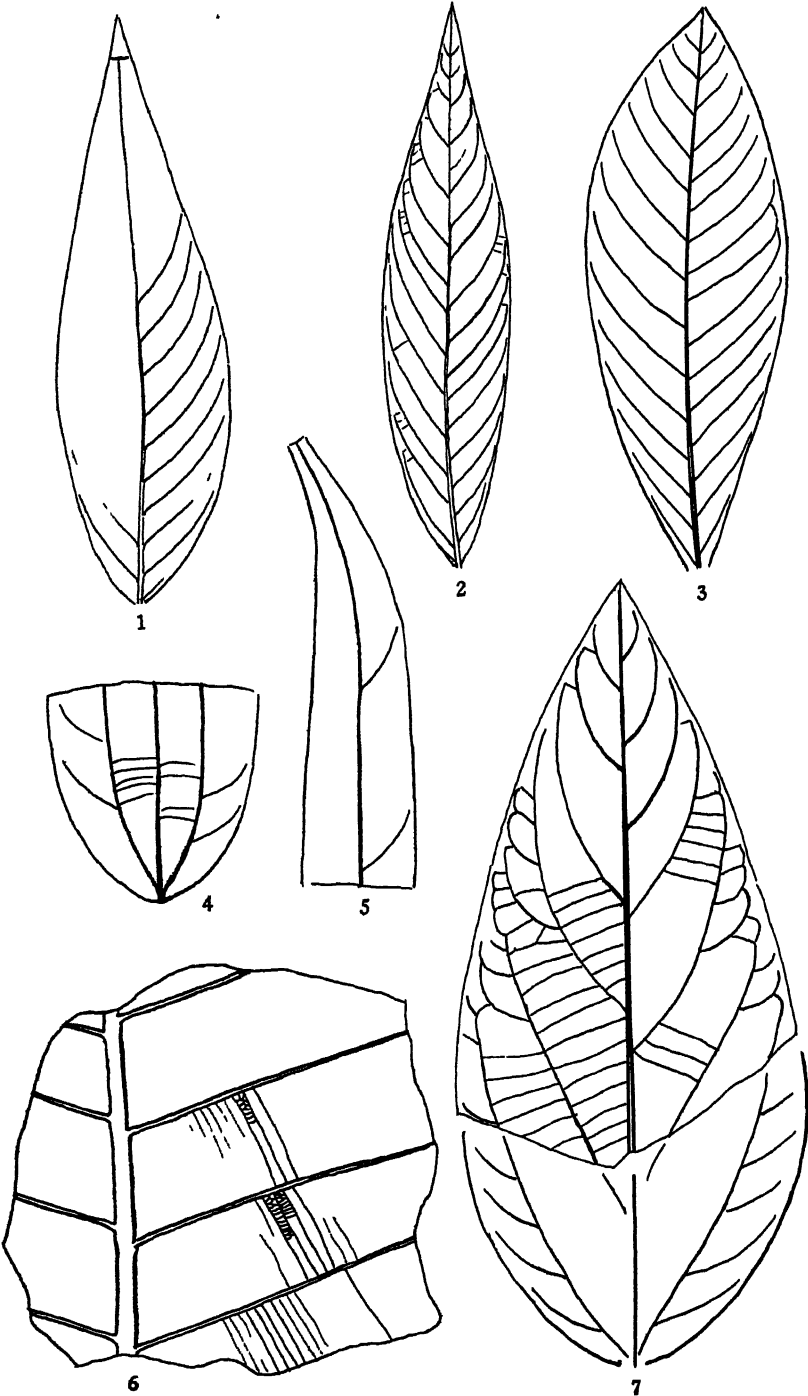
A single markedly apiculate tip of a *Ficus* leaf proves to be identical with

Explanation of plates

Plate 2

- Fig. 1. *Ficus talamancana* Berry
- Fig. 2. *Persea coriacea* Engelhardt
- Fig. 3. *Couroupita santanderensis* Berry, n. sp.
- Fig. 4. *Posoqueria columbiana* Engelhardt





BERRY: MIOCENE PLANTS

a species from the Middle Miocene of southern Costa Rica, which was based upon material showing both surfaces of the whole leaf.

Leaves large, elliptical in general outline. Tip apiculate-acuminate, the acumen upwards of 3 centimeters in length. Base decurrent. Margins entire, full and evenly curved. Texture subcoriaceous. Length ranging from 14 to 16 centimeters. Maximum width ranging from 5.5 to 7 centimeters. Petiole stout. Midvein very stout, prominent on the under side of the leaf, relatively narrow on the upper side. Secondaries below the tip 8 or 9 subopposite to alternate pairs, diverging from the midvein at wide angles, 75 to 80 degrees, relatively straight and subparallel until they approach the margins where they are camptodrome. Tertiaries thin.

This handsome form may be matched by existing species in both hemispheres among the very numerous species of this cosmopolitan genus.

Occurrence: Station 35 S., 25 W.

Ficus cf. *betijoquensis* Berry

Text-figure 2, No. 2

A small but rather characteristic basal fragment of a leaf from Station 27 N., 2 E. probably represents this species, but in view of its incompleteness is not positively determined. The species was described⁵ originally from Betijoque, Venezuela.

Genus *COUSSAPOA* Aublet

Coussapoa sp.

Plate 3, Figure 6

Small but characteristic fragments of leaves of this genus are present at two localities in the De Mares Concession. Since the features which permit the generic identification of fragments is the character of the tertiary venation, and since this is very similar in the different species, no specific determination is possible.

Species have been described in recent years from the Miocene or Pliocene of Mexico,⁶ Colombia,⁷ Venezuela,⁸ Trinidad,⁹ Ecuador¹⁰ and Bolivia.¹¹

⁵ Berry, E. W. Proc. U. S. Natl. Mus. 59: 566, pl. 108, fig. 5, 1921.

⁶ Berry, E. W. Proc. U. S. Natl. Mus. 62, art. 19, p. 6, pl. 2, 1923.

⁷ ——— Idem. 75, art. 24, p. 4, pls. 3, 4, 1929.

⁸ ——— Idem. 59: 563, fig. 2, pl. 108, figs. 1-4, 1921.

⁹ Hollick, A. Bull. N. Y. Bot. Garden 12: 296, pl. 6, fig. 1, 1924; Berry, E. W., Johns Hopkins University Studies in Geology No. 6, p. 86, pl. 1, fig. 4, 1925.

¹⁰ Berry, E. W. Idem. No. 10, p. 99, pl. 3, fig. 9, 1929.

¹¹ ——— Idem. No. 4, p. 168, pls. 4, 5, 1922.

Plate 3

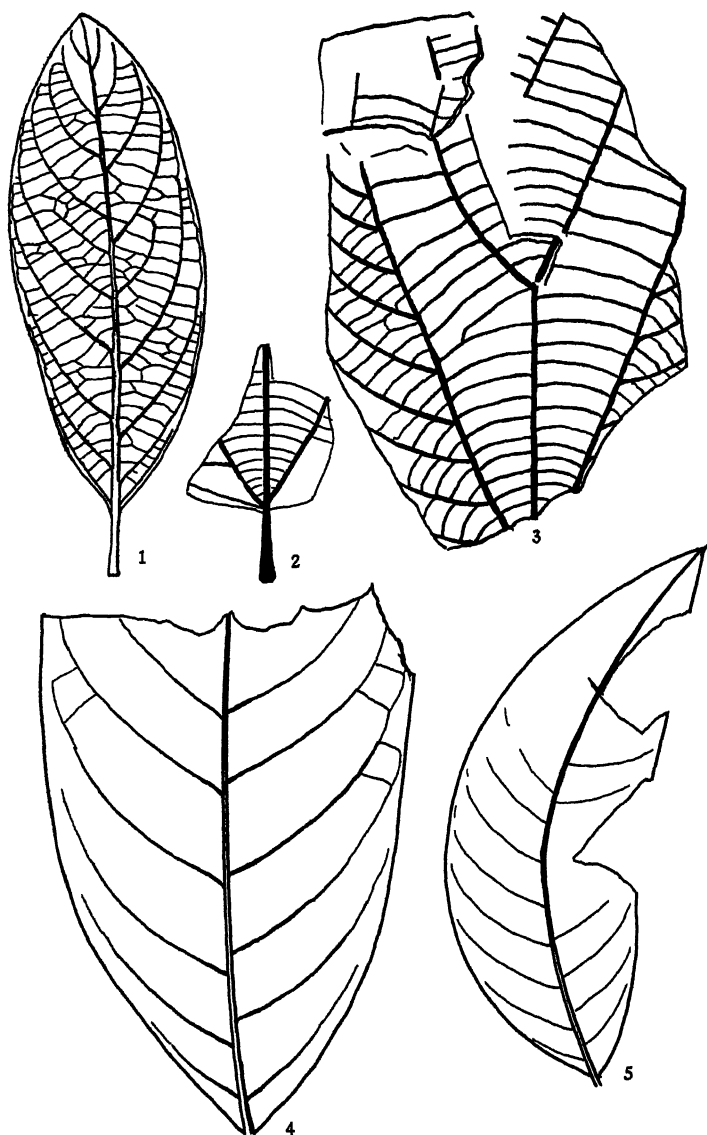
Figs. 1-3. *Avicennia miocenica* Berry, n. sp.

Fig. 4. *Buettneria* sp.

Fig. 5. *Phyllites* sp.

Fig. 6. *Coussapoa* sp.

Fig. 7. *Hernandia Tongi* Berry



Text-figure 2

- No. 1. *Mespilodaphne colombiana* Berry, n. sp.
2. *Ficus* cf. *betijoquensis* Berry
3. *Hernandia Tongi* Berry
4. *Anona* cf. *Guppyi* Berry
5. *Tapirira lanceolata* Engelhardt

Among these the present fragments appear to be most like *Coussapoa villosoides* Berry from near Betijoque in the State of Trujillo, Venezuela, and Lower or Middle Miocene in age.

The genus contains about 15 existing species of shrubs and trees confined to the tropical rain forest from southern Mexico to the Bolivian Yungas and Brazil.

Occurrence: 27 N., 2 E. and 35 S., 25 W.

Order ANONALES
Family ANONACEAE
Genus ANONA Linné
Anona cf. *Guppyi* Berry
Text-figure 2, No. 4

A specimen showing about half of a leaf from Station 27 N., 2 E. is very close, if not identical, with *Anona Guppyi* described originally¹² from the Miocene of Betijoque, Venezuela. I believe it to be this species but in view of its incompleteness hesitate to so identify it. A fragment is also present at Station 35 S., 25 W.

Order SAPINDALES
Family ANACARDIACEAE
Genus TAPIRIRA Aublet
Tapirira lanceolata Engelhardt
Text-figure 2, No. 5

Tapirira lanceolata Engelhardt, Abh. Senck, naturf. Gesell. 19: 15, pl. 9, fig. 4, 1895; Berry, Proc. U. S. Natl. Mus. 55: 291, pl. 15, fig. 1, 1929.

This species was described by Engelhardt from the Interandean basin of Loja in southern Ecuador in deposits which are late Miocene or Pliocene in age, and what appears to be the same species occurs in the Lower Miocene Zorritos formation in northwestern Peru.

It belongs to a small genus of existing shrubs and trees with odd pinnate leaves, not otherwise known in the fossil state, confined to the South American tropics, and was compared by its describer with the existing *Tapirira guianensis* Aublet.

Occurrence: 27 N., 2 E.

Order PARIETALES
Family GUTTIFERAE
Genus RHEEDIA Linné
Rheedia miocenica Berry

Rheedia miocenica Berry, Johns Hopkins University Studies in Geology, No. 6, p. 109, pl. 5, fig. 3, 1925.

This species was described from the porcellanite of Siparia, Trinidad, B. W. I. A complete specimen occurs in the collection from 35 S., 25 W. The

¹² Berry, E. W. Proc. U. S. Natl. Mus. 59: 567, figs. 1-4, 1921.

genus is distinguished with difficulty from the related genus *Calophyllum*. The existing species are arborescent and confined to the region between the Antilles, eastern Peru and Rio de Janeiro, Brazil. The only other fossil species known comes from the Pliocene of Bahia, Brazil.

Order MALVALES
Family STERCULIACEAE
Genus BUETTNERIA Linné
Buettneria sp.
Plate 3, Figure 4

This fragment from Station 27 N., 2 E. appears to represent the genus *Buettneria* but is too incomplete to be properly characterized. It is rather similar to a form from Santa Ana, Colombia, described by Engelhardt as *Buettneria cinnamoniifolia*¹³ and is also not unlike a form from Loja, Ecuador, which this author referred to the Lauraceous genus *Camphoromoea*.

The genus embraces about 50 existing species, the majority of which are found between the Antilles and northern Argentina. Fossil species are known from the Eocene onward.

Order LAURALES
Family HERNANDIACEAE
Genus HERNANDIA Linné
Hernandia Tongi Berry, n. sp.
Plate 3, Figure 7; Text-figure 2, No. 3

Leaves of medium to small size for this genus, ovate in outline, with a broadly rounded base and an acuminate tip. Margins entire. Texture subcoriaceous. Length ranging from 10.5 to 17 centimeters. Maximum width, at or below the middle, ranging from 4.5 to 9 centimeters. Petiole not preserved. Midvein stout and prominent on the under side of the leaf. Lateral primaries one on each side, opposite, stout and prominent, diverging from the midvein at acute angles at a greater or less distance above its base, ascending and dying out subparallel to the lateral margins one-half or two-thirds the distance to the tip. Secondaries mediumly stout, alternate to subopposite, 3 to 5 pairs, diverging from the midvein at angles of 45 degrees or less, ascending in regular sweeping curves, camptodrome.

From the outer side of the lateral primaries there are numerous, stout, regularly and closely spaced, camptodrome secondaries which diverge at acute angles and are subparallel. Tertiaries well marked, comprising closely spaced and mostly simple veins at right angles to the primaries and secondaries.

This is a type of Tertiary leaf which has frequently been referred to the genus *Ficus*, as for example in the case of the *Ficus mississippiensis* group of

¹³ Engelhardt, H. Abh. Senck. naturf. Gesell. 19: 32, pl. 7, fig. 9, 1895.

the Eocene in the United States,¹⁴ but which probably is not related to *Ficus*. It is also very similar to the leaves of entire *Sterculias*. Several or all of these may profitably be compared with the modern species of *Hernandia*.

The present fossil form is represented by very incomplete material from Station 27 N., 2 E., but is better known from more complete material from La Victoria, State of Zulia, Venezuela, from which the foregoing description is largely drawn. The specific name is in honor of Jas. A. Tong, one of the collectors of the Venezuelan material.

This species may be matched by the leaves of the existing *Hernandia guianensis* of northern South America. The genus contains ten or a dozen existing species of climbing shrubs in the tropics of both hemispheres and is not otherwise known in the fossil state.

Family LAURACEAE
Genus PERSEA Gaertner fils
Persea coriacea Engelhardt
Plate 2, Figure 2

Persea coriacea Engelhardt, Abh. Senck. naturf. Gesell. 19: 26, pl. 6, figs. 3, 4, 1895.

Berry, U. S. Natl. Mus. Proc. 75, art. 24, p. 9, pl. 5, fig. 3, 1929.

The material upon which the present identification is based indicates a leaf somewhat larger than the type, but in view of the well known variation in size of the leaves in individual species of this genus this is not a serious factor.

The species was described from the Tertiary of Santa Ana in Colombia and was compared by its describer with the existing *Persea rigida* Nees—a Brazilian species. It was subsequently recorded from Leiva, Department of Boyaca, Colombia. To me it seems more like the leaves of the existing *Persea gratissima* Gaertner found from Mexico and the Antilles to eastern Bolivia, and now cultivated in all tropical and subtropical regions.

Engelhardt described several large and rather similar fossil leaves from Colombia, referring them to several species of *Nectandra* and *Persea*, and it is almost if not quite impossible to separate them in any objective way.

The age of the flora found near Santa Ana in Colombia has never been determined beyond its being of Tertiary age, although it is certainly not older than Miocene.

Occurrence: Station 35 S., 25 W.

Genus MESPILODAPHNE Nees
Mespilodaphne colombiana Berry, n. sp.
Text-figure 2, No. 1

Leaves of medium size, oval in outline, widest medianly and tapering about equally distad and proximad. Apex abruptly pointed. Base broadly cuneate,

¹⁴ See Berry, E. W. U. S. Geol. Survey Prof. Paper 131, pp. 9-12, 1922.

minutely decurrent. Margins entire and evenly rounded. Texture subcoriaceous. Length between 7 and 8 centimeters. Maximum width about 3 centimeters. Petiole stout, about 1 centimeter in length. Midvein stout, prominent, curved. Secondaries stout, prominent, 7 or 8, somewhat irregularly spaced and mostly alternate pairs they diverge from the midvein at angles around 45 degrees, are regularly curved, ascending, and die out as diminishing arches parallel with the margins. Tertiaries well marked, percurrent across small areas and inosculating over larger ones; where the secondary spacing is wider than the average a subsecondary may intervene.

Of course one cannot be too certain in the generic identifications among the Lauraceae, and I have seen *Perseas* very similar to the present form, but try to be consistent with the practise laid down in my studies of the Eocene floras of southeastern North America.

I find it objectionable to follow the usage of modern systematists and lump *Oreodaphne* and *Mespilodaphne* in one genus (*Ocotea*).

Occurrence: 27 N., 2 E.; 19 N., 2 W.; 35 S., 25 W.

Order MYRTALES
Family MYRTACEAE
Genus EUGENIA Linné
Eugenia comparabilis Hollick

Eugenia comparabilis Hollick, Bull. N. Y. Bot. Garden 12: 310, pl. 8, figs. 2-5, 6b, 1924; Berry, Johns Hopkins University Studies in Geology, No. 6, p. 119, pl. 9, figs. 1-5, 1925; Hollick, Sci. Survey of Porto Rico. vol. 7, pt. 3, p. 216, pl. 55, figs. 5b, c; pl. 79, figs. 3 c, d; pl. 80, fig. 1, 1928.

This species is a common element in the porcellanite of Siparia and the Forest Sand of Trinidad, B. W. I., and in the Collazo shales of the Lares district in Porto Rico. Hollick could reach no more definite conclusion in regard to the Collazo shales than that they were Lower Middle Tertiary in age, but I should say that this single species, if correctly identified, proves their Miocene age.

Occurrence: Station 27 N., 2 E.; 19 N., 2 W.; 35 S., 25 W.

Family LECYTHIDACEAE
Genus COUROUPITA Aublet
Couroupita santanderensis Berry, n. sp.
Plate 2, Figure 3

Leaves of medium size, oblong-ovate or slightly oblong-obovate, abruptly pointed at both ends, the base slightly narrower than the tip. Margins entire. Texture coriaceous or subcoriaceous. Length about 14.5 centimeters. Maximum width about 4 to 4.5 centimeters. Petiole missing, obviously stout. Midvein stout, prominent, slightly curved. Secondaries thin, prominent numerous subparallel; they diverge from the midvein at wide angles which de-

crease distad at regular intervals for the most part and are camptodrome. Tertiaries mostly obscured, a few percurrent ones visible. Where two secondaries are more widely spaced there will be an intermediate subsecondary and this may occur once or twice in a single leaf.

The genus contains ten or a dozen existing species of trees ranging from the Lesser Antilles and Central America through northern South America to eastern Peru and south central Brazil. The only other fossil form known to me is *Couroupita ovata* Hollick and Berry¹⁵ of the Pliocene of Bahia, Brazil. Both may be compared with the leaves of *Couroupita guianensis* Aublet and *Couroupita surinamensis* Martius of northern South America.

Occurrence: Station 35 S., 25 W.

Order PERSONALES
Family VERBENACEAE
Genus AVICENNIA Jacquin
***Avicennia miocenica* Berry, n. sp.**
Plate 3, Figures 1-3

Leaves under the average size of those in the existing black mangrove; variable in form, being narrowly ovate, broadly lanceolate or sometimes slightly obovate. Apex varying from acuminate to bluntly pointed. Base rounded to rather narrowly cuneate. Margins entire. Texture coriaceous. Length ranging from 7.5 to 8 centimeters. Maximum width ranging from 1.75 to 2.6 centimeters. Petiole not preserved. Midvein stout and prominent. Secondaries numerous, stout, subparallel, camptodrome; their angle of divergence dependent on the form. Tertiaries mostly obsolete.

The genus contains over 30 existing species cosmopolitan in tropical regions on muddy tidal shores. It appears in the lower Eocene of southeastern North America, and the existing black mangrove, *Avicennia nitida* Jacquin is common in the Pleistocene of Trinidad, B. W. I. What is probably a third fossil occurrence of *Avicennia* is a leaf from Santa Ana in Colombia described by Engelhardt¹⁶ as a species of the Myrtaceous genus *Jambosa* Rumphius—an Oriental type. This differs strikingly from *Avicennia miocenica*.

Occurrence: Station 27 N., 2 E.

Order RUBIALES
Family RUBIACEAE
Genus POSOQUERIA Aublet
Posoqueria columbiana Engelhardt
Plate 2, Figure 4

Posoqueria columbiana Engelhardt, Abh. Senck. naturf. Gesell. 19: 40, pl. 7, fig. 8, 1895.

¹⁵ Hollick, A. & Berry, E. W. Johns Hopkins University Studies in Geology, No. 5, p. 90, pl. 10, fig. 5, 1924.

¹⁶ Engelhardt, H. Abh. Senck. naturf. Gesell. 19: 35, pl. 9, figs. 6, 7, 1895.

This species was described by Engelhardt from near Buga in the Cauca valley, Colombia, from beds of unknown Tertiary age. It was compared with the existing *Posoqueria latifolia* Roemer & Schultes which is still a native of Colombia, ranging from Panama to the Guianas and southward. It is present in some abundance but in a mostly very fragmentary condition at the plant locality 35 South, 25 West.

The genus contains between 5 and 10 species of shrubs or trees in Central and northern South America.

Incertae Sedis

Phyllites sp.

Plate 3, Figure 5

Fragments of a lanceolate leaf without generic characters are present at Station 27 N., 2 E.

THE JOHNS HOPKINS UNIVERSITY
BALTIMORE, MARYLAND

Invasion by *Marchantia polymorpha* following forest fires

PAUL W. GRAFF

Botanical literature bearing upon the ecology of the liverworts in North America is decidedly meager. For the most part this literature seems to be confined to short scattered statements and brief notes. The real value of these must remain in more or less doubt until they have been correlated, or materially supplemented by further investigations. It would seem that our bryologists, thus far, have been more interested in the morphology and taxonomy of the Hepaticae than in their intrinsic value or their economic status in the community.

As a whole there is such a limited quantity of real data available that any fair judgment regarding the environmental relationships of these liverworts must, at least for the present, be held in abeyance. The lack of interest thus evidenced in the ecological features relative to this group would seem to be due to a prevailing idea that the Bryophyta as a whole are of only minor biological importance. The evidence upon which this opinion is based is both scanty and inconclusive. More data are required, and as these accumulate it is possible that this view may be changed. The field is an open one, and it is to be hoped that in time some student of this group may be encouraged to engage in its exploration.

Brinkman (1929) has reported briefly on the habitat preferences of certain liverworts. It is pointed out in his paper that these plants seem to have considerable value as ecological guides in the interpretation of forest conditions. He concludes that members of the Hepaticae may be very useful, and that they play an important role as indices of moisture conditions and of the ultimate capacity of forest sites.

Griggs (1933) has made a study of revegetation in the region of Katmai Volcano, in the Valley of Ten Thousand Smokes. Sterile ash thrown up during the eruption of 1912 was found to be entirely free from vegetation when visited in 1919. Later, in 1930, he found extensive areas of this same ash covered with a pure stand of leafy liverworts, so dense as to form a thick matted carpet. The evidence showed that the districts thus invaded had not been contaminated by any flowage of water from surrounding areas and were entirely lacking in humus. Two species, *Lophozia bicrenata* (Schmid.) Dumort. and *Cephaloziella byssacea* (Roth) Warnst., both members of the leafy Hepaticae, were recognized as the sole invaders, and of these two the latter was seemingly the more important. It is stated that "ordinary plants" are unable to colonize undisturbed deposits of pure ash,

apparently because of a lack of nitrogen. The ash in this instance was found to be practically nitrogen-free. By means of culture experiments, Griggs was able to show that *Cephaloziella* "was able to grow, at least for a time, upon media as nearly free from nitrogen compounds as it is possible to prepare." He concludes that these two species are particularly adapted to this environment because of their small need for soil nitrogen.

Two recent papers by Torrey (1932) were published with the object of recording the early invasion, and seemingly uncontested spread, of *Marchantia polymorpha* over areas denuded of vegetation by forest fires. In the first of these he reports the finding "of large, widely spreading mats of the liverwort *Marchantia polymorpha*, upon thin soil barely covering the ledges, after an almost complete destruction of the previous vegetation" by an extensive forest fire during the preceding autumn. This occurred on the south end of Kittatiny Mountain in Warren County, New Jersey.

In his second equally brief article Torrey quotes from a letter in which W. W. Diehl, of the United States Bureau of Plant Industry, reports having observed this same species of liverwort "in some places covering an acre or more" within an area that had been burned over the previous year. The locality in this case was on Old Rag Mountain, in Virginia. In this same article it is also mentioned that a similar phenomenon had been observed on Long Mountain, in the Harriman section of the Palisades Interstate Park, west of Bear Mountain in New York. No data are given concerning the general conditions of these several habitats. One is led to believe that the burning over of the areas is considered the chief contributory cause of the phenomenon.

This recently reported pyrophilous character of *Marchantia* is not an unknown condition, but one that seems to have escaped prominent mention in the literature. Previously, for example, we find that Durand (1908), in describing the usual habitat of *Marchantia polymorpha*, says that it grows commonly on damp soil in ravines or along wood-roads. But to this statement of usual occurrence, he adds that its best development is reached on damp burned soil. By way of illustration he cites a visit made to a "burntout swamp several acres in extent in which the ground was nearly completely covered with luxuriant thalli to a depth in some places of several inches."

These reports regarding *Marchantia* have been of special interest to me because of similar occurrences that I have observed in the western portion of the United States. Such phenomena are not uncommon, according to my experience, in the mountainous regions of western Montana, particularly in that portion west of the continental divide. There, however, whenever I have found *Marchantia polymorpha* overspreading large areas of

burned-over soil, distinctive humidity and soil conditions were found to prevail.

This pyrophilous nature of *Marchantia* was first strikingly brought to my attention in July of 1924 while I was engaged in making a survey of timber diseases in the Montana state forest north of the town of Whitefish, in Flathead County. This forest area includes Stryker Ridge and the adjacent country of the Stillwater and Whitefish River drainage, and is located in the northwestern portion of the state but a few miles south of the Canadian border. It was the seemingly unusual extent of the area occupied, as well as the nature of the habitat, that attracted my attention.

Subsequently I observed other localities where a similar condition appeared. The best of these was in the valley of the Belmont, a tributary of the Blackfoot River, in the extreme eastern portion of Missoula County. A third instance, also worthy of note, was observed in the valley of one of the upper forks of Dead Man's Gulch, in the Bitter Root Mountains, in the extreme southern portion of Missoula County.

A fourth circumstance was found in the Mission Mountains, on the east side of Flathead Lake, in Lake County. This was in a locality where the fire had occurred several seasons previous to my visit. The conditions in this case had advanced to a point where they were of a much less pronounced character than in the three previously mentioned. The inroad of other plant life had materially changed the scene, and while *Marchantia* was still plentiful other plants were interspersed with it. Conditions were such, however, that one could easily look back through the changes that had taken place and, in the light of conditions observed on Stryker Ridge, the Belmont and Dead Man's Gulch, see the steps by means of which the change had progressed.

The instances previously reported by Torrey from the eastern states, while in mountainous districts, occurred at a comparatively low altitude. He tells me that his Kittatiny Mountain site was at an altitude of from 1,200 to 1,450 feet while that on Long Mountain was at from 800 to 1,100 feet. My western examples occurred at from 3,500 feet to approximately 6,500 feet elevation. The Stryker Ridge site was located at an elevation of somewhere between 3,500 and 3,800 feet. That on the Belmont and the one in the Bitter Root Mountains were both at an elevation of approximately 4,500 feet. There is no intention to assume anything exceptional for these elevations as they are within the perfectly normal range for *Marchantia* in the region under consideration. The highest site in which I observed the pyrophilous habit was that seen in the Mission Mountains. This was at approximately 6,500 feet elevation. It seems doubtful to me if altitude, within reasonable limits, is of any special significance as a deter-

mining factor in the distribution of *Marchantia polymorpha*, though naturally a matter of general interest. The lower river valleys in that portion of Montana situated west of the Continental Divide are at an approximate elevation of 3,000 feet, and this species is quite prevalent in the vicinity of shaded forest streams from that altitude to near the upper forest limits.

The features held in common by the Stryker Ridge, Belmont, and Dead Man's Gulch sites were the invasion, growth and spread of *Marchantia polymorpha* over an area of unusual size, and to the exclusion of other plants, under strikingly similar environmental conditions. The sites in these three instances were located in protected pockets among steep-sided mountains. They had been completely burned over during the period of fire hazard the year preceding my observations. The physical properties and humidity conditions of the soil were practically identical.

The Mission Mountain site, while not in one of these protected mountain pockets, presented otherwise essentially similar features. It was located in a wide saddle, between two mountain peaks, that extended from a point looking down upon the Swan River Valley on the east to one overlooking the Mission Valley on the west. It was short, however, as the steep opposing mountain slopes to the north and south were not far distant from one another. The side of the saddle toward the Mission Valley had been dammed by a morainal deposit, and as a result a well-protected high-altitude lake had been formed. Becoming gradually filled and changed into a marsh-meadow, its soil and humidity characteristics were not essentially different from those of the mountain pockets of the other localities.

The conditions at Stryker Ridge were typical of the several cases that came under my observation. The vegetation of this site, which included somewhat over two acres, and for some considerable distance about, had been severely burned and apparently destroyed. Beyond this the timber destruction must have included about one hundred acres. What had been previously a closely protected mountain marsh-meadow inhabited by the usual grasses and their associates had had these replaced by a dense matted growth of *Marchantia polymorpha*. In looking over the situation there seemed to have been two important factors contributing to the phenomenon, if we may call it such, of *Marchantia* invasion. The peculiar environmental conditions and the morphology of the hepatic seem to have been in close harmony with one another.

One finds many instances of these mountain meadows of varying size, closely surrounded by steep, densely forested hillsides, forming secure pockets among the mountains of the northwest. All of these pocket meadows show evidence of having been at one time the location of small

mountain lakes. These were slowly filled during the course of years. The resulting accumulation is composed, to a considerable depth, of the remains of marsh plants, and above these of meadow plants. These plant remains are mingled with silt and a large amount of fine gravel washed from the steep surrounding hillsides. A considerable quantity of this latter material is brought down by snow slides and the soil slides that habitually occur during the alternate freezing and thawing of spring. The resulting mixture that fills up the lake forms a soil porous enough for good aeration and drainage but with a sufficient quantity of fibrous humus to ensure also a good moisture-holding capacity.

Deep winter snows collect in these pockets and, due to the protection afforded, last later in the spring than the snow on the surrounding slopes. With the melting of this deep snow deposit, and contributions from the higher snow fields, these areas become flooded and remain in a more or less marshy state until early summer. The last rains of spring occur in this region during the early part of June, and no more may be expected until the latter portion of September. The few thunder showers of this summer period are fleeting and furnish comparatively little lasting moisture. The excessively moist period of spring is thus followed by a summer of drought.

The area covered by the growth of *Marchantia* was comparatively level. Despite the violence of the fire, apparently there had been sufficient moisture in the soil at that time to prevent the entire destruction of humus. The surface was thoroughly burned over, but no deeply penetrating "ground fire" persisted to cause, as frequently happens during serious fires, the utter destruction of this necessary soil component. While comparatively level there was, however, provision for efficient but slow drainage. A small stream, with its surface a foot or so below the general ground level, flowed from the upper to the lower end of the meadow.

Marchantia polymorpha is not an uncommon plant within the northern Rocky Mountain region, especially in the vicinity of the numerous forest streams. The "seeding" of the area in question may easily have occurred from plants growing along the stream banks either above or below the burned over meadow.

Spore dispersal is accomplished by means of air currents. In the narrow mountain valleys of this vicinity air drainage is very pronounced and regular in its flow. Breezes habitually blow down the canyons during the night and early morning hours, then reverse and flow upward throughout the day and early evening. As these breezes are regularly recurring, and often of considerable strength, plants above or below the fire area may have contributed their spores to the denuded tract. Spore distribution normally takes place prior to the season of fall rains. It is evident from the

densely matted growth produced that this "seeding" must have been followed by a period of rapid development. The moist nature of the denuded soil during the early autumn and the naturally reduced competition were favorable factors.

With respect to its reproductive period *Marchantia* is decidedly hydrophilous. The organs of reproduction are able to carry out their activities only in the presence of moisture. The antherozoids are motile, and the plants are heterothallic. As a consequence plants of this species are not found except in localities where moisture is plentiful at the requisite season.

On the other hand, *Marchantia polymorpha* is vegetatively xerotherous. This is a decisive factor in its ability to maintain itself in this mountain area. Throughout this region, as I have already mentioned, dry periods of about three months duration normally occur as a seasonal characteristic between June and September. Numerous liverworts and mosses possess this xerotherous habit, an essential to them because of their custom of forming a thin surface layer without material soil penetration.

The quantitative relationship of solutes in the soil to the determination of its habitants is known only to a very limited extent, though admittedly an important factor. Seaver and Clark (1912) have shown that the soluble matter in soils may be increased materially with heating. They have also shown that certain flowering plants are retarded in their growth by this concentrate, but that cryptogamous plants, with their ability to adapt themselves to nutrients of a comparatively high degree of concentration, may respond favorably to such an environment. While this is particularly true of numerous well-known species of fungi, it is also a recognized feature of certain Bryophyta, notably among the mosses. It would seem that *Marchantia polymorpha* may also be included within this category. Seedlings of *Pinus contorta*, *Epilobium angustifolium* and other seed plants characteristic of the floras of burned areas had become established on the adjacent well-drained slopes but had not invaded the marsh-meadow area. The line of demarcation between the *Epilobium* and *Marchantia* formations was very sharp. This condition could not be classed as an exception for, it must be emphasized, the Stryker Ridge, Dead Man's Gulch, and Belmont sites were all similar in this respect.

It will be readily seen that conditions in the several localities I have mentioned were particularly adapted to "seeding" by *Marchantia*, and to the subsequent growth of this plant. If the seeds of other plants present in the surface soil had been killed by the fire early competition would have been minimized. Even if these were not entirely disposed of, their development was, without doubt, inhibited because of the factor just mentioned above. The extensive growth of fireweed and seedlings of lodgepole pine

upon the surrounding slopes of this confined area could hardly be accounted for unless there had been a distribution of their seeds over the entire area. It would seem that we have here very definite evidence and good cause for assuming, in the case of these recognizedly pyrophilous plants, growth inhibition in the burned-over marsh-meadow area.

On the Mission Mountain site of several years standing herbaceous and shrubby flowering plants had become interspersed about the area. These were largely disposed as colonial bays and islands. It is possible that some of these were remnants of the former flora but, from their age and disposition, more probably represented a slow invasion of the locality.

Mosses, of which the genus *Funaria* appeared to be the most prevalent representative, were present in some quantity. Members of several other moss genera were seen, but these, for the most part, were of comparatively minor importance. *Polytrichum* was occasional in drier places near the side slopes. As these mosses may be classed among the pyrophilous plants, it would seem probable that they formed the second troop of invasion, and entered after *Marchantia* had effected some slight change in the surface conditions. While these mosses require a certain amount of periodical humidity they do not care for the extreme moisture conditions tolerated by *Marchantia*.

These mosses were generally disposed about the bays and islands of flowering plants, and to some extent appeared among them. Occasional islets of moss alone were present among the *Marchantia*. Wherever these intrusions were observed, the spot was found to possess somewhat less humidity than its immediate surroundings. In some of these instances a boulder was located a few inches beneath the surface, but such circumstances were by no means universal or even in the majority.

A dense stand of young lodgepole pine occupied the mountain slope adjacent to the southern margin, but had not invaded the marsh area. From this slope the fireweed had almost entirely disappeared because of the denseness of the tree growth. The opposite slope to the north was composed of steep rocky cliffs that afforded little security for trees. It was largely barren rock up which the fire had not passed for any great distance.

It seemed apparent that the development of this Mission Mountain area was more backward than might be expected, and there appeared to be two evident reasons for this condition. A small stream flowed through the marsh-meadow in the case of the Stryker Ridge, Dead Man's Gulch, and Belmont sites. In this instance there was no stream present, and drainage was effected by means of seepage through the coarse gravel of the moraine at the western boundary. For this reason drainage would be slower than in these other cases. Below the moraine, on the outer side, the seepage water

accumulated in sufficient quantity to form a small stream that flowed down the mountain side. Because of the general reaction to conditions there was some considerable evidence that here a swamp, rather than a marsh, might be the final result.

The second reason for retarded development was the matter of altitude. At approximately 6,500 feet the growing period of the more restricted flowering plants was much shortened. *Marchantia*, on the other hand, would not be as greatly influenced by this altitude. Associated with this shortening of the seasonal growth period was another factor of some little importance. The meadow lay in the shadow cast by the mountain peak to the south during the middle and warmer portion of the day. This again would have less effect on the *Marchantia* than on the secondary invaders.

The Belmont site was visited a second time two seasons after its burning. Some slight change was being effected, and it was found that grasses were encroaching upon the *Marchantia* along the stream bank. The *Marchantia* was also showing thin spots here and there through the area, and in these localities colonies of moss were found to be developing. In some of the larger of these moss colonies evidence of grass growth was beginning to appear, though in these places such plants were not yet evident in any great quantity. The most pronounced indications of reversion toward the pre-fire condition were seen at the upper end of the area. Here, both near the stream and from either side of it toward the margin of the marsh, grasses were making a determined effort to return. There were no signs of weediness apparent anywhere in the area.

The Lodgepole pines were developing rapidly on the surrounding hill-sides, and while *Epilobium* (*Chamaenirion*) was still in evidence it was being gradually crowded out by other growth. Neither the pines nor fireweed had made any progress in the invasion of the marsh-meadow. All evidence was in favor of a rapid reversion to the status quo and a healthy grass land.

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A study of the growth, transpiration, and distribution of the conifers of the Rocky Mountain National Park¹

OMER E. SPERRY
(WITH NINE FIGURES)

The Rocky Mountain National Park is a prominent forest area of the central Rocky Mountains in northern Colorado. The Park has an area of 405 square miles (U.S.D.I. 1934) and the forest is in its virgin state, undisturbed by man except in the vicinity of roads and trails.

The rates of diameter increase of the conifers presented in this study have been determined from measurements of increment cores taken from approximately one thousand trees. These trees were selected from undisturbed areas which were reached from the established trails and roads within and near the Park. Growth data were secured from excavated and young trees.

In addition to the growth data, transpiration, evaporation, rainfall, and temperature data were secured and are presented to aid in the explanation of environmental conditions. The number and distribution of trees in given areas and the associated woody and herbaceous plants are also considered. These physical and distribution data were secured primarily from established stations which will be discussed in order.

Although ten members of the *Coniferae* grow within the boundaries of the Park, only five are of economic importance due to quantity and uniformity of growth. These five were selected for this study: *Pinus ponderosa* Lawson, the ponderosa pine; *Pinus contorta* Loudon, the lodgepole pine; *Pseudotsuga taxifolia* (Lamarck) Britton, the Douglas fir; *Abies lasiocarpa* (Hooker) Nuttall, the sub-alpine fir; and *Picea Engelmannii* Engelmann, the Engelmann spruce.

METHODS

Diameter measurements were obtained from cores secured with a Swedish increment borer during the summer of 1932. Some cores were also taken during the summer months of 1929, 1930, and 1931. When cores from the latter were used they were corrected so as to involve corresponding growth rings. One core was taken from the north and one from the south side of the chosen tree at breast height, approximately four and one-half feet from the ground line. These were marked n and s, wrapped, and taken into the field laboratory for further examination.

To secure measurements from the cores in the laboratory each was clamped in a specially designed vise and the surface representing the trans-

¹ Contributions from the Department of Botany, University of Nebraska, N. S. No. 97.

verse section was shaved with a sharp scalpel to obtain a clearer view of the growth rings. The growth rings were counted with the aid of a binocular microscope and were separated into ten-year periods, beginning at the cambial end. The thickness of the wood formed in each ten-year period was then measured in millimeters and recorded. After both north and south radii were recorded the thickness of the wood formed during each ten year period on the diameter of the tree was determined.

Height and diameter measurements were secured from the standing trees. Height was determined in feet by use of the Faustmann hypsometer, the stick method, or by estimations from nearby previously measured trees. Diameter measurements were taken at breast height (4.5 ft.) with a diameter tape and recorded in inches.

Soil temperatures were taken with Centigrade thermometers lowered into wooden tubes which were sunk into the soil to the depth of one foot. A large cork was placed over the bulb end of the thermometer for protection and to help govern rapid changes which might occur due to exposure at the time of reading. The tubes were covered with large rocks and insulated above with tufts of grass.

Evaporation data were obtained with round, white bulb Livingston atmometers placed in the various stations so that the bulbs were less than a foot above the surface of the soil.

Transpiration data were obtained by following the scheme of McLean (1919). Test tubes 100×25 mm. were fastened by means of a copper wire to ropes stretched between two trees at ground and five-foot levels. The test tubes were filled with water and the cut shoot, after being severed under water, was placed in the tube. The test tube was filled to about one-half inch of the top and then covered with a film of olive oil to prevent evaporation and to seal the branch as it extended from the water. After this apparatus was set up and a short time allowed for adjustment, the water level in the tube was marked on the outside of the glass. Water was added after periods of exposure with a pipette graduated in cubic centimeters and the amounts transpired were thus recorded. At the end of the exposure period the twigs used were wrapped in waxed paper and taken into the laboratory. Here the needles were carefully removed from the branches and their green weights obtained. The needles were later dried at 105°C. to obtain dry weights. From these figures the amount of water given off in grams per hour was calculated.

Crown projection maps were made of 100×100 foot plots in lodgepole pine, ponderosa pine, and Douglas fir areas. These maps or "crown mosaics" were constructed similarly to those worked out by Burns (1929). The mapping was done by dividing the plot into 10×10 foot squares.

A six-foot pole with six-inch gradations was used as a measuring device to place the tree in its exact location within the plot. Eight radial projections were made to determine the perimeter of each crown. As these measurements were made they were recorded on a scaled field chart in their exact relations. Shrubs and herbs were also recorded as each 10×10 foot plot was being mapped.

THE STATIONS: TREE AND SHRUB DISTRIBUTION:
HERBACEOUS PLANTS WITHIN THE STATIONS

Stations were established in typical areas of the lodgepole pine, ponderosa pine, Douglas fir, and Engelmann spruce-sub-alpine fir. Throughout the discussion which follows they will be referred to as the lodgepole pine station, the ponderosa pine station, the Douglas fir station, and the Engelmann spruce station. These stations were located on slopes which drained toward Fall River and within a radius of two miles of our field laboratory.

The lodgepole pine. The lodgepole pine station was located on the north face of Deer Mountain at an elevation of 8725 feet. The ages of the trees of the station ranged from 55 to 65 years; most of those examined critically were 64 and 65 years old. Careful examination of increment cores from a number of Douglas firs at the base of the slope revealed burn scars for 76 and 95 years back. This indicates that the area was burned in 1837 and again in 1856.

The lodgepole pine is the most common tree of the Park. The elevation at which the tree is usually found ranges from 7500 to about 9500 feet. This species sometimes grows in stands so dense that the plants can hardly be classed as trees, resembling rather so many large weeds. Areas of this type have developed through the excellent seeding conditions that follow fires. Mason (1915) has made counts of representative lodgepole areas and has calculated as many as 50,000 live trees per acre with heights of 8 to 10 feet. On another area he counted 101,000 live trees and 7900 dead ones, or an initial stand of 108,900 trees to the acre with heights of about 4 feet. Clements (1910) made counts of 56 trees to the ten-meter quadrat in the area of Longs Peak and Twin Sisters Mountains. This figures more than 50,000 trees to the acre. Stands of this nature are by far too dense and many of the trees are bound to succumb by gradual retardation and suppression.

In the 100×100 foot area of the lodgepole pine station as many as 14 trees were counted in an area 10×10 feet. The stand in the station as a whole was not so dense, however, and the plotted area supported 218 live trees. Five of these were small limber pines, *Pinus flexilis* James, two

Douglas firs, and 211 lodgepoles. This calculates 949 trees to the acre, which is a very good number if evenly distributed. Mason (1915) places the initial seedlings for a good stand at 1500 to 2000 to the acre. The lodgepole pine makes a better pole when the trees grow closely enough together to cause self pruning but not too close to greatly retard the tree growth.

Figure 1 is the crown mosaic map of the Deer Mountain lodgepole pine station. This sketch gives a definite picture of the distribution of the trees and shrubs within the area. The lodgepole crowns actually cover 44.93% of the ground. This could be construed to mean that when the sun was directly above this section of the forest about 55% of the ground would be exposed to the direct sunlight. Even with this large percentage of exposed ground, there is some crowding due to the chance positions of the trees. Measurements of the overlapping area for this station reveal that 2.22% of the 44.93% is again covered by two or more trees.

The distribution of the woody undergrowth found in the station is shown in the crown projection map (fig. 1). The species recorded are kinnikinnick, *Arctostaphylos Uva-ursi*²; New Jersey tea, *Ceanothus Fendleri*; *Jamesia americana*; the wild rose, *Rosa Sayi*; the red currant, *Ribes cereum*; the buffalo berry, *Shepherdia canadensis*; the elderberry, *Sambucus microbotrys*; the mountain snowberry, *Symphoricarpos racemosus*; and the wild gooseberry, *Ribes saxosum*. The Rocky Mountain maple, *Acer glabrum*, although not present within the station, was growing near by. The sprawling juniper, *Juniperus communis*, could be classed as an undershrub and is found in most forest areas at elevations below 9000 feet.

The lodgepole pine station has the least amount of herbaceous growth of any of the stations mapped. The number of species recorded for this station is not extensive, but indicates the types usually found in similar lodgepole pine areas. The species recorded are: *Arnica cordifolia*, *Chamaenerion angustifolium*, *Frasera speciosa*, *Oreochrysum Parryi*, *Pyrola minor*, *Solidago missouriensis*, *Solidago decumbens*, and *Thermopsis divaricarpa*.

The ponderosa pine. The ponderosa pine is the most common conifer in the foothills and at lower elevations. It grows in scattered groves or as isolated individuals, most commonly on the south and west slopes, at elevations ranging from 7000 to 9000 feet.

Our station was located on the gradual south slope of McGregor

² The New Manual of Botany of the Central Rocky Mountains by Coulter and Nelson, Plants of Rocky Mountain National Park by Ashton, Trees and Shrubs of Colorado by Longyear, and Check List of the Forest Trees of the United States by Sudworth have been used in the selection of names.

Mountain at an elevation of 8325 feet. The warm south slope, the open uneven-aged stand, and numerous outcrops of boulders found in this area are typical of ponderosa pine habitats. A number of older trees at the station are fire scarred, and a core taken from one of these contained five

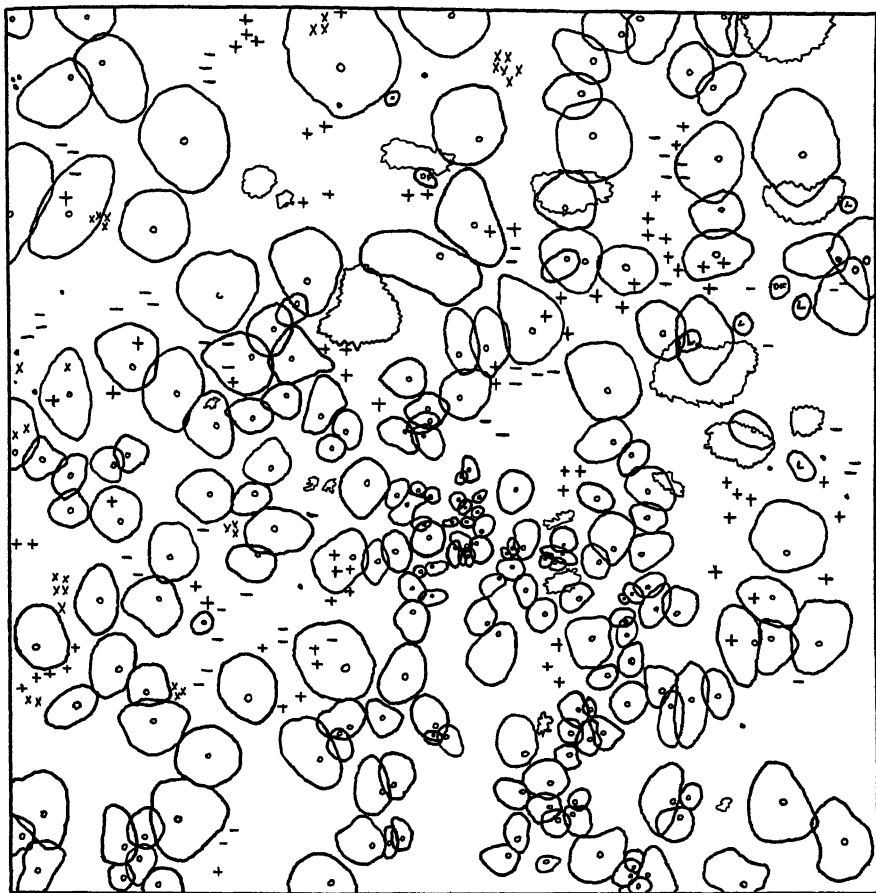


Fig. 1. Crown mosaic of the trees in the lodgepole pine station. The area mapped is 100×100 feet. The small circles indicate the positions of the trunks of the trees, and the irregular lines around these, the perimeters of the crowns. The lighter very irregular areas indicate dwarf junipers. L indicates limber pine, DF, Douglas fir. The symbols are used as follows: +, species of *Ribes*; *, mountain snowberry and elderberry; x, kinnikinnick; —, wild rose.

resin masses which indicated as many fires or burn injuries. Several trees had open scars at their bases on the north and northeast sides indicating that a ground fire, probably fanned by a north wind, had been severe. The latest date for a fire that could be set from these burn scars was 1790.

In a survey made by the author in 1929 (Sperry, 1934), a ponderosa pine south slope station of 44,000 square feet was found to contain 121 trees or 106 per acre. About 85% of the trees present were ponderosa pines and 69% were over 5 feet tall. Most of the 31% under 5 feet in height were rock growers and older trees. A west slope station of mixed pon-

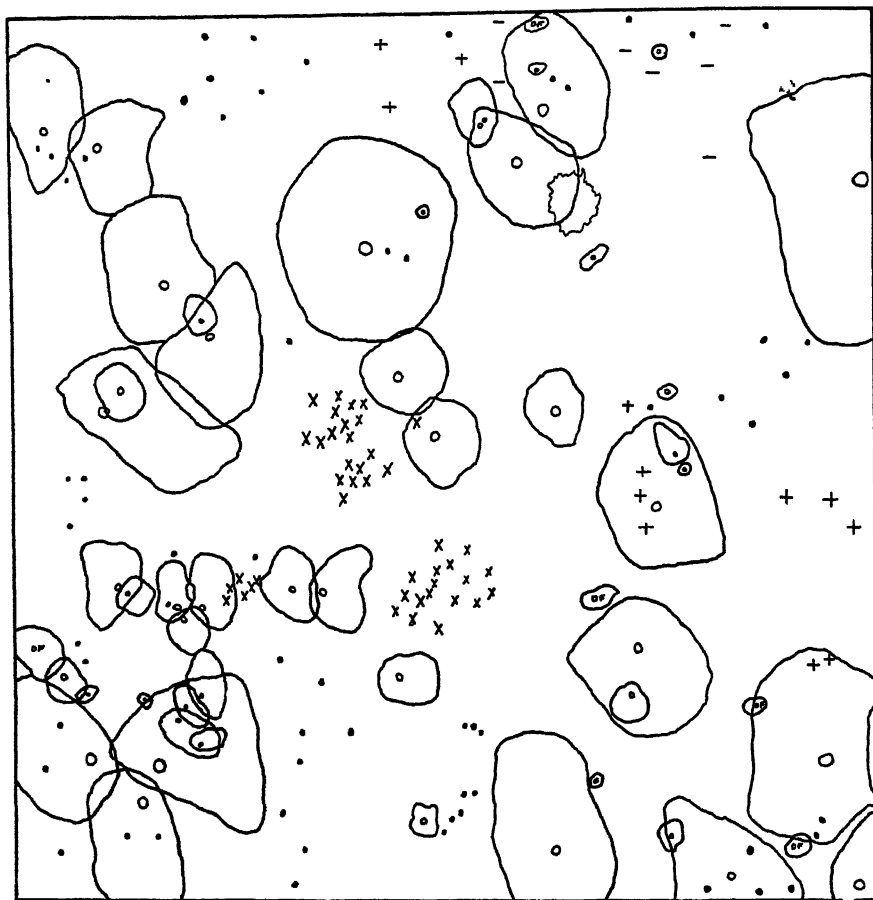


FIG. 2. Crown mosaic of the trees in the ponderosa pine station. The area mapped is 100×100 feet. The small circles indicate the positions of the trunks of the trees, the irregular lines around these, the perimeters of the crowns. Dwarf junipers are indicated by the lighter irregular lines. DF indicates Douglas fir. The symbols are used as follows: ·, antelope bush; ×, kinnikinnick; +, species of *Ribes*; -, wild rose.

derosa pine and Douglas fir, 19,750 square feet in area, supported 90 trees or 190 per acre. About 50% of these were ponderosa pine and 15% were young trees less than 5 feet tall.

The McGregor ponderosa pine station (see fig. 2) contained 59 trees or 257 per acre. About 12% of the 59 were Douglas firs and 31% were under 5 feet in height. A number of the lesser trees in this tract were small, twisted rock growers but many more young trees were found than in the station referred to above.

The open forest nature represented by the ponderosa pine station shows the most exposed ground and the least overlapping of crowns. The crowns cover 35.08% of the ground surface and 1.87% is again covered by two or more trees. This overlapping is chiefly due to young trees growing under older trees, as opposed to the overlapping of older trees in the lodgepole pine station.

This station, even with much exposed ground and an open nature, supported the least shrubby undergrowth. The most common was the antelope bush, *Purshia tridentata*. *Jamesia americana* was found in the more protected sites where moisture could be obtained. *Rosa Sayi*, *Ribes cereum*, *Ribes saxosum*, *Ceanothus Fendleri*, and *Arctostaphylos Uva-ursi* were also growing in the mapped area. *Acer glabrum*, although not common on dry south slopes, was present in the vicinity.

The ponderosa pine station had the largest number of herbaceous plants of the three stations mapped. This same relation holds true for the entire ponderosa pine range when compared to that of the Douglas fir and lodgepole pine.

The following are the flowering plants, excluding grasses and sedges, that were present in the mapped area of this station: *Achillea lanulosa*, *Antennaria aprica*, *Apocynum androsaemifolium*, *Arabis Drummondii*, *Artemisia frigida*, *Astragalus flexuosus*, *Erigeron compositus*, *Erigeron flagellaris*, *Erigeron glandulosus*, *Eriogonum umbellatum*, *Erysimum asperum*, *Fragaria ovalis glauca*, *Gaillardia aristata*, *Galium boreale*, *Geranium Fremontii*, *Lithospermum angustifolium*, *Oxytropis bilocularis*, *Pentstemon humilis*, *Potentilla rubricaulis*, *Pseudocymopterus montanus*, *Pulsatilla hirsutissima*, *Sedum stenopetalum*, *Thermopsis divaricarpa*, and *Tithymalis robustus*.

The Douglas fir. The Douglas fir station was established on a slope which drained into Big Horn Creek. The elevation of the station was 8650 feet and the slope faced east of north. The trees of this station presented an average situation for normal development. The lesser trees in the station and in most Douglas fir areas are young trees as opposed to many abnormal and rock growing types which appear as the smaller trees in the ponderosa pine areas.

In an average 50×50 foot plot in an area east of the Park boundary 110 Douglas firs were counted: about 1916 to the acre. Fifty per cent of

these were less than 6 inches in diameter and less than 8 feet tall. In a plot of the same size along upper Big Horn Creek, 44 trees were counted, 766 per acre; 25% of this count were below 6 inches in diameter. The 100×100 foot area of the Douglas fir station supported 128 trees, or 592 to the acre: 23% of these were less than 5 feet in height.

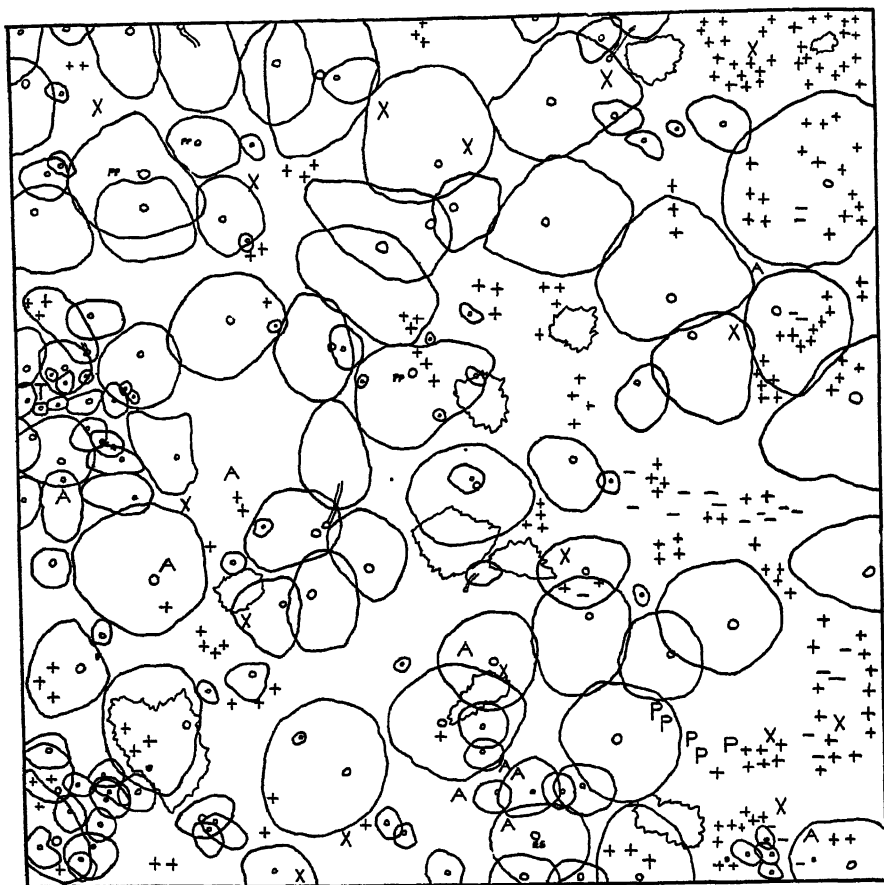


Fig. 3. Crown mosaic of the trees in the Douglas fir station. The area mapped is 100×100 feet. The small circles indicate the positions of the trunks, the irregular lines around these, the perimeters of the crowns. Sprawling junipers are indicated by the lighter irregular areas. PP indicates ponderosa pine; ES, Engelmann spruce. The symbols are used as follows: A, Rocky Mountain maple; P, chokecherry; X, *Jamesia americana*; +, species of *Ribes*; -, wild rose; *, mountain snowberry.

The crown mosaic (fig. 3) pictures the distribution of all woody plants in the Douglas fir station. The trees of this station shade more ground than was shaded in either the lodgepole or ponderosa pine stations. The

vertical projections of the crowns cover 57.51% of the surface of the station. There was 7.40% of overlapping due almost entirely to younger trees growing in the shade of the established members.

The Douglas fir station supported the greatest amount of woody undergrowth. All woody plants of the two preceding stations except the antelope bush were duplicated here. The larger plants were more numerous, especially the Rocky Mountain maple. The only shrubs found in addition to those mentioned for the other stations were the western chokecherry, *Prunus melanocarpa*, and the arrowwood, *Viburnum pauciflorum*.

The Douglas fir area had the greatest quantity of herbaceous undergrowth. In comparison, the ponderosa pine station had more species but less amount of plant growth. The lodgepole pine station ranked below both these stations in numbers of species as well as quantity of undergrowth. The following are the herbaceous plants, except grasses and sedges recorded for the Douglas fir station: *Arnica cordifolia*, *Claytonia rosea*, *Clematis columbiana*, *Drymocallis fissa*, *Fragaria ovalis glauca*, *Galium boreale*, *Heuchera bracteata*, *Oreochrysum Parryi*, *Pentstemon humilis*, *Saxifraga austromontana*, and *Washingtonia obtusa*.

The Engelmann spruce and sub-alpine fir. The Engelmann spruce station was set up about a mile upstream from the Douglas fir station in an area approximately a quarter of a mile above the lower limits of the spruce-fir belt. The elevation of the station was 9000 feet.

The Engelmann spruce form extensive forests on the slopes and along the mountain streams at elevations ranging from 8500 feet to timberline. The sub-alpine fir also grow within this range and in admixture with the spruce. The Engelmann spruce forest, as a type, reaches its lowest range along streams and waterways. Individuals of the two species are found at elevations as low as 8000 feet.

Seedlings and saplings of the spruce and fir are abundant within these forests. In an area of 9 square feet in Wild Basin 42 specimens less than 1 foot high were counted and only 6 were productions of the current season. At this rate there could be over 200,000 seedlings and young trees to the acre in addition to the established members.

In a 50×50 foot area in Hidden Valley, 128 spruce and fir were counted or 2230 per acre. Of these 128 trees, 59% were less than 6 inches in diameter, and about 85% of the total were sub-alpine firs; 35% of the 128 were less than 1 foot high (discounting the current year's seedlings) and only 2 of these were Engelmann spruce. In another plot further down the slope very similar results were obtained. The trees in the Engelmann spruce station were not so dense as in the Hidden Valley area and figured only 1390 trees to the acre with 36% less than 5 feet tall, not counting the current season's seedlings.

DIAMETER INCREASE

The study of increment cores taken from the north and south radii of sample trees yield data on the rate of growth after the tree has reached breast height. The figures for the rates of diameter increase are based on the count and measurement of the annual rings from the periphery toward the center. If the core reaches the center, the ring count will give the age of the tree above that level. Decreased diameter growth does not neces-

TABLE 1

The average diameter increase per decade of the five most prominent conifers of the Rocky Mountain National Park. The measurements are in millimeters.

DECADE	PONDEROSA PINE	LODGEPOLE PINE	DOUGLAS FIR	ENGELMANN SPRUCE	SUB-ALPINE FIR
1923-32	15.77	14.38	13.41	14.21	13.48
1913-22	19.75	19.28	20.61	15.67	16.27
1903-12	21.21	20.21	19.49	15.59	17.84
1893-1902	20.47	23.62	17.70	15.85	18.25
1883-92	19.41	26.32	11.55	15.71	16.41
1873-82	15.24	25.30	10.71	13.87	13.65
1863-72	18.80	15.11	11.28	12.77	15.60
1853-62	11.64	11.20	9.52	12.91	14.42
1843-52	17.63	12.17	10.11	11.53	13.73
1833-42	21.06	14.88	12.51	12.97	14.15
1823-32	15.33	12.14	13.24	13.09	14.06
1813-22	13.36	10.26	12.68	12.28	14.74
1803-12	15.48	12.77	16.40	12.75	14.01
1793-1802	15.20	14.95	20.09	13.98	14.39
1783-92	13.78	15.88	20.79	14.94	13.52
1773-82	15.28	9.71	19.55	14.58	10.41
1763-72	15.43	19.94	18.90	12.96	10.13
1753-62	14.35	18.54	16.00	12.74	9.78
1743-52	13.33	16.67	* 8.00	11.76	7.58
1733-42	15.04	16.83	* 5.12	11.63	7.63
1723-32	13.48	*26.75	*16.66	10.02	* 7.67
1713-22	13.56	*31.50	*13.33	10.30	* 7.50
1703-12	13.61	*19.00	*13.33	10.77	*10.50
1693-1702	15.31		*13.00	12.45	* 4.00
1683-92	13.80		*11.33	13.85	* 5.00
1673-82	13.22		*11.33	12.71	* 5.00
1663-72	12.00		*13.33	10.25	
1653-62	13.25		*20.00	* 9.70	
1643-52	10.67			* 6.37	
1633-42	14.00			* 8.00	
Average	15.42	17.74	15.27	13.07	13.52

* Too few trees represented to be included in average.

sarily mean a decrease in volume of wood formed since the layer of wood for each succeeding season is larger and longer. Thus if the diameter increase for any year is as great or greater than for the preceding year, the total volume increment for the later year is greater.

The average diameter increase per decade for all trees measured is presented in table 1. The average decade diameter increments for all trees measured are given as "average" in this table. These averages are not for the same total number of years and range from 180 years for the Douglas fir to 300 years for the ponderosa pine.

Since young trees, under favorable conditions, grow more rapidly in diameter than older trees of the same species, comparisons of growth are made on a basis of diameter-age classes. Classes of trees made in this manner are of an arbitrary nature since growth, either with old or young trees, is a steadily fluctuating variable. Diameter-age classes have thus been created with 100 growth rings (D.B.H.) as the division line so that a more direct comparison in the rates of diameter increase of old and young trees can be made.

The lodgepole pine. The lodgepole pine grew the most rapidly by forming 17.74 mm. of wood on the diameter per decade or 1.77 mm. per year. This is based on the last 200 years (or less) of diameter growth of 254 trees. The average 10-year diameter increase for all lodgepoles with less than 100 growth rings is 24.00 mm. or 2.4 mm. per year. Comparative to this figure, the lodgepole pines with more than 100 growth rings formed 9.49 mm. of wood on the diameter per 10-year period or 0.95 mm. per year. This variation from young to older trees is more marked for the lodgepole pine than for any of the other species studied. The oldest ring count obtained for this species was 239 years but very few trees measured approached the 200 year count. The older trees are either relicts of former stands that were swept by fire or members of an older stand as in the case of a few specimens measured near Bear Lake and in Wild Basin.

The ponderosa pine. The ponderosa pine ranks second to the lodgepole pine in diameter growth with an average of 15.42 mm. of diameter increase per decade or 1.54 mm. per year. Borings from 233 trees were measured as a basis for this determination.

The ponderosa pine and the lodgepole pine have very similar average rates of diameter growth when corresponding periods of time are compared. The last century, 1833 to 1932, netted an average of 18.10 mm. of diameter growth per 10-year period for the ponderosa pine and 19.25 mm. for the lodgepole pine. The preceding century, 1733 to 1832, netted 14.66 mm. for the ponderosa pine and 14.87 mm. for the lodgepole pine, when compared on the same basis. These figures show that the lodgepole

pine has a slightly greater rate of diameter increase than the ponderosa pine and the comparison on a 200-year basis indicates that the former species has a diameter increase of 14.87 mm. per 10-year period as compared to 14.66 mm. for the ponderosa pine.

Ponderosa pine trees less than 100 years old grew more rapidly than the lodgepole pine of the same diameter-age class and an average of 24.57 mm. of wood was formed per decade. The more than 100-year old lodgepole pine trees grew much slower than the ponderosa pines of the same diameter-age rank. The lodgepole formed 9.49 mm. of wood on the diam-

TABLE 2

*Millimeters of diameter increase for trees with more than one hundred growth rings (D.B.H.)
and for trees with less than one hundred growth rings (D.B.H.).*

DECADE	PONDEROSA PINE		LODGEPOLE PINE		DOUGLAS FIR		SUB-ALPINE FIR		ENGELMANN SPRUCE	
	MORE THAN 100	LESS THAN 100	MORE THAN 100	LESS THAN 100	MORE THAN 100	LESS THAN 100	MORE THAN 100	LESS THAN 100	MORE THAN 100	LESS THAN 100
1923-1932	9.36	22.0	6.65	15.32	9.20	17.78	10.64	19.08	10.41	20.05
1913-1922	14.64	24.14	8.06	20.59	13.31	28.48	12.08	24.52	11.88	25.96
1903-1912	16.21	26.31	8.43	22.48	10.46	29.67	13.33	26.61	13.23	25.66
1893-1902	16.02	26.11	8.79	25.98	11.63	29.60	15.89	29.57	13.29	27.57
1883-1892	15.45	24.44	8.67	30.50	9.62	18.52	13.63	27.24	13.67	27.27
1873-1882	11.26	25.10	10.56	26.07	9.57	17.54	11.35	28.89	12.25	24.30
1863-1872	16.63	23.94	19.41	29.09	10.60	22.20	14.35	30.40	12.35	16.70
1853-1862	9.76	22.08	10.20	16.67	9.43	16.00	14.00	22.33	12.25	19.89
1843-1852	15.63	27.59	10.86	18.00	10.03	16.00	13.73		11.26	16.60
1833-1842	21.00	24.00	13.22	25.25	12.51		14.15		12.97	
Average	14.60	24.57	9.49	24.00	10.67	21.75	13.32	26.06	12.36	22.67

eter per 10-year period and the ponderosa pine formed 14.60 mm. of wood during the same comparative period. The older class of ponderosa pine thus shows a decrease of about 42% in its rate of diameter growth when compared to the younger class of the same species. This corresponding decrease for the shorter-lived lodgepole pine is about 60%.

The Douglas fir, Engelmann spruce, and sub-alpine fir. The Douglas fir stands third in diameter growth with an average of 15.27 mm. of diameter increase per decade or 1.53 mm. per year. The sub-alpine fir and Engelmann spruce average much the same with 13.52 mm. and 13.07 mm. of diameter increase per decade, respectively. These calculations are based on tabulations from the measurements of cores from 162 Douglas firs, 151 Engelmann spruces, and 101 sub-alpine firs.

The Douglas fir has the lowest rate of diameter increase for the last 100 years of the 5 trees being considered in this study and ranks closely to the Engelmann spruce and sub-alpine fir in this respect. The diameter growth per 10-year period for the last century, 1833 to 1932, for the Douglas fir was 13.69 mm., the Engelmann spruce was second low with 14.10 mm., and the sub-alpine fir third with 15.38 mm. When the rates of diameter increase for the trees with less than 100 growth rings are compared the same relative rank is held. In this case the Douglas fir averaged 21.75 mm. per 10-year period, the Engelmann spruce 22.67 mm., and the sub-alpine fir 26.06 mm.

The decrease in the rate of growth between the two diameter-age classes for the Douglas fir is about 50%. The Douglas firs with less than 100 growth rings averaged 21.75 mm. of growth per 10-year period and the older trees averaged 10.64 mm. The average diameter growth for the alpine fir with more than 100 growth rings was 13.32 mm., and for the Engelmann spruce of the same class 12.36 mm. Table 2 is a tabulation of the less than 100 growth ring and the more than 100 growth ring diameter-age classes of the five species considered. The height and diameter measurements of the standing trees considered above are summarized in table 3.

TABLE 3

Average, maximum, and minimum heights and diameters for all trees measured and included in diameter growth figures.

SPECIES	PONDEROSA PINE	LODGEPOLE PINE	DOUGLAS FIR	ENGELMANN SPRUCE	SUB-ALPINE FIR
NUMBER OF TREES	233	254	162	151	101
Average height	33.60 ft.	33.53 ft.	37.33 ft.	48.70 ft.	43.61 ft.
Maximum height	92.00 ft.	85.00 ft.	80.00 ft.	100.00 ft.	100.00 ft.
Minimum height	10.00 ft.	15.00 ft.	12.00 ft.	12.00 ft.	10.00 ft.
Average diameter	13.33 in.	6.49 in.	11.28 in.	12.19 in.	8.62 in.
Maximum diameter	41.20 in.	19.50 in.	48.00 in.	34.25 in.	19.25 in.
Minimum diameter	2.50 in.	2.00 in.	2.25 in.	2.50 in.	2.25 in.

HEIGHT GROWTH

A number of small trees were examined to determine the rate of height growth for trees less than 4.5 feet in height. In addition to these, three older lodgepole pines were excavated and examined critically for rates of height growth. The data secured from the seedling and sapling study are presented in table 5. In most of these ring counts microscopic mounts had to be made due to the narrow rings.

The lodgepole pine. The lodgepole pine, with its ability to invade areas

deforested by fire, has the most rapid rate of growth. Figure 4 shows a diagrammatic longisection of a lodgepole pine from both north-south and east-west views. This figure shows the behavior of one of the three average trees which were dug out of the lodgepole pine station. Ring counts were made for each tree from the transition root-stem zone at the ground line upwards at 3 foot levels. The tree represented in this sketch grew very slowly until it had attained a height of three feet, the rate of growth was then more than doubled until a height of 12 feet was reached, after which the rate decreased as the tree approached its present state of maturity. All the trees thus examined showed this same general tendency in their rates of height growth (see table 4).

TABLE 4

Ring count at three-foot levels of three lodgepole pine trees.

LEVEL IN FT.	RING COUNT—YEARS			
	TREE 1	TREE 2	TREE 3	AVERAGE
Ground	65	64	64	64.3
3	58	57	59	58.0
6	55	50	57	54.0
9	52	42	55	47.3
12	48	38	49	45.0
15	43	33	43	37.7
18	38	24	34	32.0
21	29	16	6	17.0
24	19			
27	5			
Tree ht. in feet	27.58	25.58	22.0	25.0

Seedling establishment and growth are essential to the continuation of any forest area. If the trees present cannot reestablish themselves the stand will be replaced by a more adaptable species. This situation exists in the case of the lodgepole pine which seeds itself most effectively in open exposed areas. If the stand is dense or moderately so, shade is undoubtedly the factor in the failure of the lodgepole to reestablish itself. This intolerant nature has been shown by Korstian (1925) in the effects of shade on nursery stock. An illustration of the retarding nature of the established forest over seedlings can be made by considering the rate of growth of tree number 22 from table 5. This tree was 55 years old and only 4 feet high, while the older trees, which had become established ten years earlier, averaged about 27 feet in height. The older tree, illustrated in figure 5, required 7 years for the first 3 feet of height growth while the smaller tree netted only 3 inches of height in 7 years. One other small lodgepole, 38

inches high, was examined. This specimen grew 1 inch per year for the first three years and continued at about that same rate until it was over one foot high. After that the rate of growth was gradually retarded and 16 years were required for the second and third feet of height growth.

TABLE 5

Ring count from the ground line upward at three to twelve inch levels to determine rate of growth for young trees. S.F. indicates sub-alpine fir, E.S., Engelmann spruce, D.F., Douglas fir, P.P., ponderosa pine, and L.P., lodgepole pine.

	SPECIES	HEIGHT IN INCHES	DIAMETER AT GROUND LINE IN INCHES	AGE AT GROUND LINE	AGE AT 3 INCH LEVEL	AGE AT 6 INCH LEVEL	AGE AT 9 INCH LEVEL	AGE AT 12 INCH LEVEL	AGE AT 18 INCH LEVEL	AGE AT 24 INCH LEVEL	AGE AT 36 INCH LEVEL	AGE AT 48 INCH LEVEL
1.	S.F.	1.25		5								
2.	S.F.	2.5		11								
3.	S.F.	4.5	.094	10	2							
4.	S.F.	5.0	.187	13								
5.	S.F.		1.63	48	44	40						
6.	S.F.	10.0	.125	36	31	19						
7.	S.F.	12.0	.25	27	20	9	2					
8.	S.F.	24.0	.875	54	35	28	20	17	6			
9.	S.F.	48.0	1.125	80	70	37	34	32	25	18	8	
10.	E.S.	1.75		4								
11.	E.S.	11.0	.271	27	19	12	3					
12.	E.S.	11.0	.25	36	27	12						
13.	E.S.	12.0	.271	23	12	4						
14.	E.S.	36.0	1.125	57	52	48	44	40	20	12		
15.	E.S.	38.0	.875	63								
16.	D.F.	28.0	.562	44	35	25	19	12	7	2		
17.	D.F.	40.0	.875	47	40	32	29	27	25	13	8	
18.	D.F.	50.0	1.25	57	49	40	25	22	15	12	7	2
19.	P.P.	38.0	1.00	31	25	19	17	15	13	9		
20.	P.P.	58.0	1.75	42	38	32	23	27	19	18	10	6
21.	L.P.	38.0	.812	32	29	25	21	19	16	12	3	
22.	L.P.	48.0	1.125	55	48	44	40	36	25	22	9	

The ponderosa pine. The seedlings of the ponderosa pine are very scarce in this area and one seldom finds a current season's seedling. They do occur, however, as young trees are present, but to a lesser degree than seedlings of neighbor species.

One tree 38 inches and one 58 inches high were examined to obtain facts regarding the rates of growth for trees under 4.5 feet in height. The shorter tree was 31 years old and the taller 42 years, according to ring

count. On the average, 5 years were required for the first 3 inches of height growth, 6 years for the second 3 inches, 3 years for the third 3 inches, and 1.5 years for the fourth 3 inches. Thus, there was an increase in the rate of growth as the trees became established. The first foot of height was reached during the fifteenth and sixteenth growing seasons. This acceleration in the rate of growth continued and the second foot of height was reached during the twenty-second and twenty-fourth growing seasons.



Fig. 5. Seedlings of *Abies lasiocarpa*. A, cotyledonary stage; B, two years old; C, early in third growing season; D, four years old. These specimens were collected in the Engelmann spruce station.

The Douglas fir. Three trees were obtained to illustrate the rate of growth for young Douglas firs. They averaged 37 inches high and 47 years old. The average first 3 inches of height was attained in 8 years, the second 3 inches in 9 years, the third 3 inches in 8 years, and the fourth 3 inches in 4 years. The first foot of height was reached in 29 years and the second in an additional 11.3 years. The seedlings, thus, did not exhibit the rapid and steady increase in the rate of growth that the ponderosa pine did.

The Engelmann spruce and sub-alpine fir. The sub-alpine fir examined averaged 8.83 years in attaining the first 3 inches of height, 13.4 years for the second 3 inches, 5.67 years for the third 3 inches, and 2.5 years for the fourth 3 inches. The slow rate of growth of the sub-alpine fir is illustrated in figure 5 which is a photograph of four seedlings, 1, 2, 3, and 4 years old. The Engelmann spruce seedlings examined grew faster than the above sub-alpine fir and averaged 16.75 years for the first 6 inches of height growth.

ENVIRONMENTAL CONDITIONS

The only available data on rainfall and temperature were those collected at the Colorado Public Service Station in cooperation with the United States Weather Bureau. This station is located on the valley floor at the base of the south slope of McGregor Mountain about three-fourths mile below the location of the ponderosa pine station. The records were not complete for every month from 1928-1932 due to a change of station location and a loss of some records.

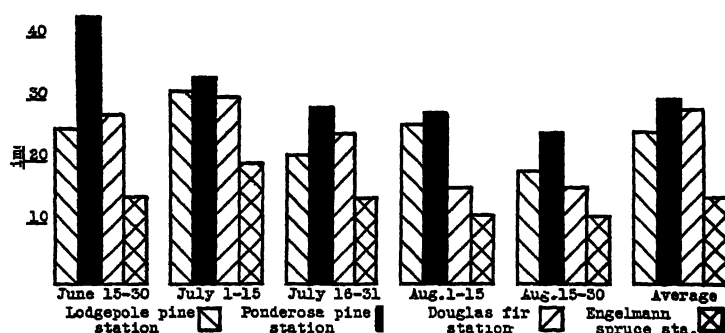


Fig. 6. A graphical representation of evaporation from atmometers during fifteen-day periods in the four stations.

The average annual rainfall recorded for the five-year period (see table 6) was 12.99 inches. Since these records were taken near the ponderosa pine station we may conclude that the species in this area receive about 13 inches of rainfall annually. The most moisture falls during the months of March, April, July, and August. January and December are the driest months of the year.

The lowest temperatures recorded at this station were in March, but the cold periods were usually of shorter duration than those of the three or four preceding winter months. The average maximum and the maximum high temperatures for June, July, and August showed little variation. July had the highest average maximum temperature and August the greatest daily range.

Evaporation data, measured by means of Livingston white bulb atmometers, were obtained at the four stations during the summer months of 1932. These data are illustrated graphically in figure 6. Evaporation is recorded in cubic centimeters per day; 15-day periods are compared. A greater amount of water was lost in the ponderosa pine station than in any of the other stations. The Douglas fir station ranked second, the

lodgepole pine third, and the least amount of water was given off in the area of the Engelmann spruce.

Soil temperatures were obtained only in the Douglas fir and ponderosa pine stations. The temperatures obtained from the ponderosa pine station showed a greater range than those from the Douglas fir station. This same relation existed in the air temperatures. The temperatures at one foot below the surface of the ground averaged 17.30°C. in the ponderosa pine station and 12.30°C. in the Douglas fir station. The maxima were 22°C. and 13°C., the minima in both 11°C. Thus, the greatest daily range in temperature for the ponderosa pine station was 11°C. while only 2°C. was recorded as a maximum range for the Douglas fir habitat.

TABLE 6

Temperature in degrees Fahrenheit, and rainfall in inches for 1928-1932. Records made at the Colorado Fish Hatchery 1928, and at the plant of the Colorado Public Service Company 1929-32.

MONTH	AVERAGE MAXIMUM	AVERAGE MINIMUM	AVERAGE RANGE	MAXIMUM RECORD	MINIMUM RECORD	AVERAGE RAINFALL
Jan.	33.3	14.6	21.1	52.3	0.1	0.20
Feb.	39.7	19.2	21.4	56.0	1.2	0.98
March	41.7	19.1	26.3	55.8	-12.2	2.23
April	54.1	27.5	27.6	68.0	8.3	1.03
May	59.2	31.2	27.7	78.2	15.8	0.98
June	69.3	36.0	31.3	83.0	28.0	0.93
July	77.9	50.9	32.6	88.0	32.5	2.50
Aug.	70.1	42.4	44.8	83.0	35.8	1.02
Sept.	65.6	37.6	28.9	80.0	24.0	0.66
Oct.	57.4	30.0	32.6	74.2	16.0	0.61
Nov.	40.6	19.0	23.9	61.7	- 6.7	1.55
Dec.	37.1	15.3	24.2	56.0	- 0.25	0.20
Total annual rainfall						12.99

POTOMETER STUDIES

The cut shoot (potometer) type of phytometer as described under Methods was used in this study. The volume of transpiration is very difficult to measure accurately since any man-made device for such attempts removes the tree from its normal growing conditions. Thus, potometer records are not true measures of transpiration and are used as comparative measures for the trees concerned. Shoots were exposed for short periods because longer periods cause a decrease in the rate of transpiration due to a gradual blocking of the vascular system (Maximov, 1929). The most valuable information from such an instrument, according to Maximov, is obtained just after the cutting of the shoot.

The potometers were run at approximately two-week intervals during the summer of 1932, beginning June 16. The shoots were placed in the same positions in the same stations at each experimental period which ranged from 6 to 7.8 hours. Before setting up the experiment, trees from which the cut shoots were to be taken were located and marked. The cut shoots for all three stations were obtained from the same side of the same tree and as nearly as possible from the same level. The shoots were first taken to the lodgepole pine station with the cut ends in water and the potometers set up as previously described. After installing the apparatus in the lodgepole pine station, shoots were taken from this station to the ponderosa pine and Douglas fir stations and similar installations were made. By using a saddle horse less than two hours were needed for this

TABLE 7

The amount of water lost from potometers on June 16. The calculations are based on cubic centimeters per gram of green leaf per hour and per gram of dry leaf per hour. P.P. indicates ponderosa pine, L.P., lodgepole pine, and D.F., Douglas fir.

	SPECIES	TIME IN HRS.	CC. TRANS.	GREEN WT. G.	CC./G./HR. GREEN WT.	DRY WT. G.	CC./G./HR. DRY WT.
Lodgepole Pine Station							
5-foot level	P.P.	6	24.8	60.9	.068	32.7	.126
	L.P.	6	8.7	14.1	.103	7.2	.201
	D.F.	6	9.0	27.4	.054	14.1	.106
Ground level	P.P.	6	25.9	64.9	.067	33.9	.127
	L.P.	6	10.1	14.2	.119	7.4	.227
	D.F.	6	6.8	39.9	.028	21.6	.052
Ponderosa Pine Station							
5-foot level	P.P.	7.5	15.4	20.8	.099	10.3	.199
	L.P.	7.5	15.6	10.7	.194	4.7	.442
	D.F.	7.5	12.8	23.8	.072	11.5	.148
Ground level	P.P.	7.5	18.2	14.25	.170	7.1	.342
	L.P.	7.5	7.5	5.2	.192	2.3	.436
	D.F.	7.5	12.9	19.4	.089	9.4	.183
Douglas Fir Station							
5-foot level	P.P.	7	10.4	15.5	.096	10.3	.144
	L.P.	7	10.2	11.85	.118	4.7	.310
	D.F.	7	5.6	17.0	.044	11.5	.070
Ground level	P.P.	7	8.2	15.65	.075	7.1	.165
	L.P.	7	9.2	10.7	.123	2.3	.571
	D.F.	7	4.0	13.05	.044	9.4	.061

procedure. Water was added and the apparatus taken down in the same order. This allowed about the same amount of time for transpiration in all three stations. The transpiration data obtained for the six periods are presented in tables 7 to 12.

Wet and dry bulb readings were taken with a cog psychrometer in the three stations on the days that the potometer experiments were run. These readings were not taken at intervals sufficiently close to be of great comparative value. The temperatures were usually the highest in the ponderosa pine station, averaging 67.43°F. at 9:15 A.M. and 67.64°F. at 2:30 P.M. The average in the Douglas fir station was 65.25°F. at 9:40 A.M. and 65.42°F. at 3:45 P.M. The average in the lodgepole pine station was 55.21°F. at 8:45 A.M. and 45.00°F. at 3:00 P.M. The relative humidities

TABLE 8

The amount of water lost from potometers on July 1. The calculations are based on cubic centimeters per gram of green leaf per hour and per gram of dry leaf per hour. P.P. indicates ponderosa pine, L.P., lodgepole pine, and D.F., Douglas fir.

	SPECIES	TIME IN HRS.	CC. TRANS.	GREEN WT. G.	CC./G./HR. GREEN WT.	DRY WT. G.	CC./G./HR. DRY WT.
Lodgepole Pine Station							
5-foot level	P.P.	6	9.7	20.6	.070	8.5	.190
	L.P.	6	5.3	8.25	.107	3.0	.294
	D.F.	6	3.3	9.5	.056	4.1	.134
Ground level	P.P.	6	8.4	23.5	.060	10.1	.139
	L.P.	6	4.6	8.1	.095	2.9	.264
	D.F.	6	7.3	14.0	.087	5.4	.225
Ponderosa Pine Station							
5-foot level	P.P.	6	6.8	13.2	.086	4.3	.264
	L.P.	6	4.25	3.7	.191	1.8	.394
	D.F.	6	5.0	9.5	.088	4.3	.194
Ground level	P.P.	6	6.3	14.0	.075	5.3	.198
	L.P.	6	5.5	8.5	.108	3.4	.271
	D.F.	6	5.1	10.5	.081	4.3	.197
Douglas Fir Station							
5-foot level	P.P.	6	6.7	17.9	.062	7.3	.153
	L.P.	6	3.5	8.4	.069	3.0	.194
	D.F.	6	4.0	9.5	.070	3.7	.180
Ground level	P.P.	6	7.7	15.8	.081	6.1	.210
	L.P.	6	4.1	7.7	.089	3.1	.220
	D.F.	6	3.5	11.0	.053	3.9	.150

were not as constant nor as comparable as the temperature readings. The average low was 39.57% for 3:00 P.M. in the lodgepole pine station and the average high was 49.17% for 3:45 P.M. in the Douglas fir station.

The transpiration figures which follow are based on green weight. Calculations were made for dry weight and are included in tables 7 to 12. The ratio between dry and green weight was very constant and the latter are used in the following comparisons.

TABLE 9

The amount of water lost from potometers on July 18. The calculations are based on cubic centimeters per gram of green leaf per hour and per gram of dry leaf per hour. P.P. indicates ponderosa pine, L.P., lodgepole pine, and D.F., Douglas fir.

	SPECIES	TIME IN HRS.	CC. TRANS.	GREEN WT. G.	CC /g./HR. GREEN WT.	DRY WT. G.	CC./g./HR. DRY WT.
Lodgepole Pine Station							
5-foot level	P.P.	7.8	11.1	14.6	.097	6.9	.210
	L.P.	7.8	8.3	9.2	.115	4.5	.237
	D.F.	7.8	8.6	14.0	.079	5.8	.181
Ground level	P.P.	7.8	9.3	11.0	.108	5.0	.238
	L.P.	7.8	8.4	8.4	.128	3.7	.291
	D.F.	7.8	7.6	11.1	.088	4.6	.212
Ponderosa Pine Station							
5-foot level	P.P.	7.6	15.2	15.7	.127	7.2	.278
	L.P.	7.6	11.4	8.2	.183	3.9	.385
	D.F.	7.6	11.6	21.8	.070	9.1	.168
Ground level	P.P.	7.6	14.9	17.8	.110	8.0	.245
	L.P.	7.6	14.0	6.25	.295	2.9	.635
	D.F.	7.6	13.7	17.3	.104	6.9	.261
Douglas Fir Station							
5-foot level	P.P.	7.4	14.3	21.4	.090	9.7	.200
	L.P.	7.4	12.2	9.8	.168	4.0	.412
	D.F.	7.4	6.5	16.55	.053	7.2	.122
Ground level	P.P.	7.4	10.1	15.2	.090	7.3	.187
	L.P.	7.4	8.5	12.7	.090	5.3	.217
	D.F.	7.4	8.95	21.1	.057	8.9	.136

Transpiration comparisons within the stations. The cubic centimeters of water lost per gram of green leaf per hour at the ground and 5 foot levels have been averaged and figures 7, 8, and 9 constructed. These figures

represent the amounts of water transpired by the three species in the respective stations during the six experimental periods.

Gail (1921) exposed cut shoots of Douglas fir for periods of four hours and found that 2.89 times as much water was lost on the southwest slopes as on the northeast slopes. If we consider the ponderosa pine station as

TABLE 10

The amount of water lost from potometers on August 1. The calculations are based on cubic centimeters per gram of green leaf per hour and per gram of dry leaf per hour. P. P. indicates ponderosa pine, L. P., lodgepole pine, and D. F., Douglas fir.

	SPECIES	TIME IN HRS.	CO. TRANS.	GREEN WT. G.	CC./G./HR. GREEN WT.	DRY WT. G.	CC./G./HR. DRY WT.
Lodgepole Pine Station							
5-foot level	P. P.	6.5	14.0	28.0	.077	12.3	.175
	L. P.	6.5	8.3	10.6	.120	5.0	.254
	D. F.	6.5	5.5	11.5	.074	5.2	.163
Ground level	P. P.	6.5	11.2	22.3	.077	10.2	.109
	L. P.	6.5	7.9	11.6	.105	5.4	.225
	D. F.	6.5	7.4	9.9	.115	4.6	.247
Ponderosa Pine Station							
5-foot level	P. P.	6.5	18.1	24.8	.114	10.7	.260
	L. P.	6.5	18.3	20.2	.139	9.5	.296
	D. F.	6.5	8.6	18.8	.070	9.4	.141
Ground level	P. P.	6.5	16.5	30.5	.083	12.0	.211
	L. P.	6.5	8.0	13.6	.090	6.9	.178
	D. F.	6.5	2.7	15.6	.027	8.0	.052
Douglas Fir Station							
5-foot level	P. P.	6.5	15.4	35.0	.068	16.0	.148
	L. P.	6.5	5.5	10.5	.081	5.0	.171
	D. F.	6.5	6.7	16.2	.064	7.2	.143
Ground level	P. P.	6.5	10.7	27.4	.060	12.6	.131
	L. P.	6.5	4.2	9.8	.066	4.6	.140
	D. F.	6.5	5.3	16.9	.048	8.1	.101

comparable to the above southwest slopes and the Douglas fir station to the northeast slopes, we find 1.31 times as much water lost by the Douglas fir in the ponderosa pine station as in its own station. If the water loss of all shoots is compared, we find 1.44 times as much water lost in the

ponderosa pine and 1.16 times as much in the lodgepole pine as in the Douglas fir station.

Figure 7 shows the amounts of water transpired by the lodgepole pine in the three stations. The lodgepole pine appears to be an extravagant user of water. The response of the lodgepole pine to the conditions of the

TABLE 11

The amount of water lost from potometers on August 13. The calculations are based on cubic centimeters per gram of green leaf per hour and per gram of dry leaf per hour. P.P. indicates ponderosa pine, L.P., lodgepole pine, and D.F., Douglas fir.

	SPECIES	TIME IN HRS.	CC. TRANS.	GREEN WT. G.	CC./G./HR. GREEN WT.	DRY WT. G.	CC./G./HR. DRY WT.
Lodgepole Pine Station							
5-foot level	P.P.	7	12.7	29.9	.061	9.7	.187
	L.P.	7	12.6	15.2	.118	6.3	.277
	D.F.	7	10.2	13.1	.111	6.0	.243
Ground level	P.P.	7	31.5	23.7	.189	9.5	.474
	L.P.	7	10.8	17.3	.089	7.6	.203
	D.F.	7	7.5	12.1	.089	5.3	.202
Ponderosa Pine Station							
5-foot level	P.P.	6.7	20.4	38.2	.079	15.4	.197
	L.P.	6.7	14.3	16.2	.132	7.3	.292
	D.F.	6.7	10.0	21.4	.069	9.3	.160
Ground level	P.P.	6.7	12.9	29.4	.065	12.1	.159
	L.P.	6.7	29.3	21.6	.202	9.0	.486
	D.F.	6.7	11.2	23.1	.072	11.0	.152
Douglas Fir Station							
5-foot level	P.P.	6.7	17.0	24.9	.102	9.4	.270
	L.P.	6.7	14.8	21.2	.104	9.2	.240
	D.F.	6.7	11.3	25.3	.067	11.2	.150
Ground level	P.P.	6.7	16.4	35.8	.068	14.7	.166
	L.P.	6.7	12.0	16.6	.108	7.2	.249
	D.F.	6.7	5.2	19.2	.040	8.6	.190

environment at the three stations is also very marked and in every case the greatest amount of water was given off in the ponderosa pine station. Water lost in the lodgepole pine and Douglas fir stations varied, but the average at the end of the summer was greater in the environment of the lodgepole pine.

Figure 8 places the data obtained from the transpiration of the ponderosa pine in the various stations on a readily comparative basis. With one exception, the greatest amount of water was transpired by the ponderosa pine in its own habitat; the early and late season's losses were

TABLE 12

The amount of water lost from potometers on August 25. The calculations are based on cubic centimeters per gram of green leaf per hour and per gram of dry leaf per hour. P.P. indicates ponderosa pine, L.P., lodgepole pine, and D.F., Douglas fir.

	SPECIES	TIME IN HRS.	CC. TRANS.	GREEN WT. G.	CC./G./HR. GREEN WT.	DRY WT. G.	CC./G./HR. DRY WT.
Lodgepole Pine Station							
5-foot level	P.P.	6	16.5	30.3	.085	12.4	.222
	L.P.	6	11.0	21.3	.086	8.8	.208
	D.F.	6	8.0	21.8	.061	9.3	.143
Ground level	P.P.	6	14.2	23.7	.100	10.5	.225
	L.P.	6	8.1	17.8	.076	8.1	.166
	D.F.	6	7.2	23.8	.050	10.5	.114
Ponderosa Pine Station							
5-foot level	P.P.	6.3	13.0	22.3	.092	9.9	.208
	L.P.	6.3	11.0	21.2	.082	9.7	.180
	D.F.	6.3	6.7	17.9	.059	8.0	.133
Ground level	P.P.	6.3	18.2	22.1	.131	9.5	.304
	L.P.	6.3	18.5	32.8	.089	13.5	.217
	D.F.	6.3	8.6	24.6	.055	10.5	.130
Douglas Fir Station							
5-foot level	P.P.	6.3	16.8	20.2	.132	8.7	.307
	L.P.	6.3	12.0	23.9	.080	10.4	.183
	D.F.	6.3	8.6	19.2	.071	9.0	.152
Ground level	P.P.	6.3	13.4	27.2	.078	11.0	.193
	L.P.	6.3	8.7	30.7	.039	12.7	.109
	D.F.	6.3	5.1	20.7	.039	9.2	.089

greatest in the area of the Douglas fir, and the mid-summer losses were greatest in the lodgepole pine station. The average for the summer was slightly greater in the region of the lodgepole.

The response of the Douglas fir potometers to the three environments is shown in figure 9. The Douglas fir was most conservative in the use of water in its own station. In four out of six experiments, the greatest amounts of water were lost in the ponderosa pine area and on two oc-

casions the most was transpired in the lodgepole pine habitat. The average for the season was slightly greater in the lodgepole than in the ponderosa pine station.

This relative rank of water loss, as measured by potometers agrees in the main with the results of Bates (1923) and Pearson (1924) who used potted seedling phytometers to secure data on transpiration. The findings are also in agreement with Roeser (1932) who used seedlings in water

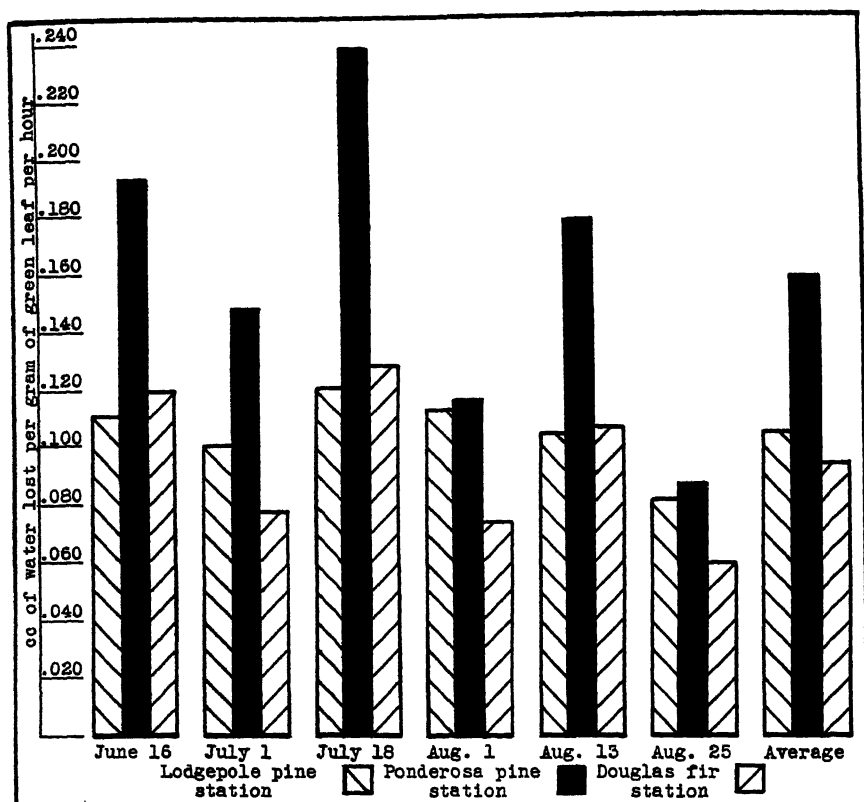


Fig. 7. A comparison of the rates of transpiration of the lodgepole pine in the lodgepole pine, ponderosa pine, and Douglas fir stations.

cultures. Gail and Long (1935) on the other hand found that the rate of water loss for potted lodgepole seedlings failed to exceed the losses recorded for corresponding ponderosa pine seedlings.

When the cubic centimeters of water lost per gram of green leaf per hour by the three species in all three stations are computed, a grand average is obtained of .120 cc. for the lodgepole, .091 cc. for the ponderosa pine, and .0663 cc. for the Douglas fir. This ranking is in agreement with

Bates (1923) in that both the western yellow (ponderosa) pine and lodgepole pine transpired more per tree than the Engelmann spruce and Douglas fir.

Roeser (1932) found that the Douglas fir showed a much smaller in-

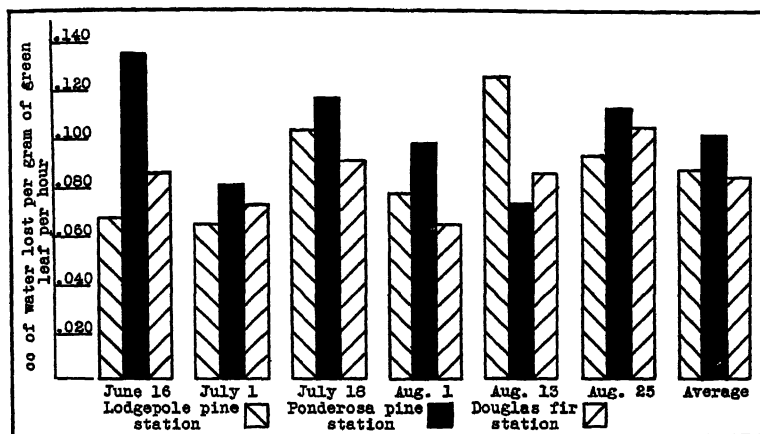


Fig. 8. A comparison of the rates of transpiration of the ponderosa pine in the lodgepole pine, ponderosa pine, and Douglas fir stations.

crease in transpiration in comparison with the other species when the habitats were varied. In our experiments the ponderosa pine fluctuated the least with an average decrease of 16.2% when placed in the lodgepole

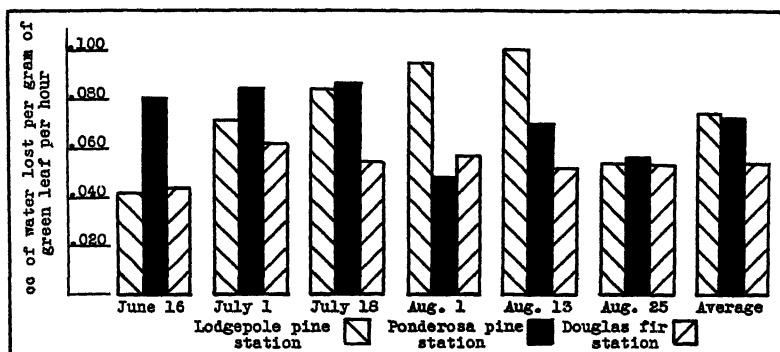


Fig. 9. A comparison of the rates of transpiration of the Douglas fir in the lodgepole pine, ponderosa pine, and Douglas fir stations.

and Douglas fir stations. The Douglas fir ranked second with an average increase of 34.2% in the habitats of the pines. The lodgepole increased its rate of transpiration 52.4% in the ponderosa pine and decreased 8.5% in the Douglas fir station.

The water loss of potometers within the stations is in the same order as water evaporated from atmometers in the respective stations. The potometer records are based on a total of 119.8 hours of exposure of six potometers in each of three stations while the atmometer records are for a total of 76 days.

CONCLUSIONS

The pines showed a greater rate of diameter increase than the other species considered. They also transpired more per gram of green leaf per hour throughout the season. Young ponderosa pines and lodgepole pines of initial stands had a faster rate of growth than the Douglas fir. We can thus conclude that the pines have a greater rate of diameter increase, a faster rate of growth, and transpire more than the Douglas fir. Since the sub-alpine fir and Engelmann spruce approach most closely the rate of growth of the Douglas fir and since the least water was given off in their habitat, we can place it in the same comparative rank with the Douglas fir.

ACKNOWLEDGMENT

The writer wishes to express his appreciation of the valuable suggestions and kindly criticisms of Dr. Raymond J. Pool, under whose direction this work was done. Thanks are also due the officials of the Rocky Mountain National Park for permission to work within the Park area, and to Mr. Jess Polling of the Colorado Public Service Company for permission to use certain rainfall and temperature data.

SUMMARY

This study is based on data secured from conifers growing within and near Rocky Mountain National Park.

The five species considered are: *Pinus contorta*, *P. ponderosa*, *Pseudotsuga taxifolia*, *Picea Engelmannii*, and *Abies lasiocarpa*.

Four stations were established; one in the lodgepole, one in the ponderosa pine, one in the Douglas fir, and one in the Engelmann spruce area. The most intensive studies were carried out in the first three stations.

Measurements on the rates of diameter increase were obtained from increment cores taken from the north and south sides of about 1000 trees. Height growth rates were determined by examining seedlings and saplings and from older lodgepole pines.

The type of forests formed by the lodgepole pine, the ponderosa pine, and the Douglas fir is shown by a study of the crown mosaics of these species. The distribution of the woody undergrowth is also recorded in these crown projection maps. Herbaceous plants are recorded for the mapped portion of these three stations.

The average diameter (D.B.H.) increase per year based on all measurements made for the various species was: lodgepole pine 1.77 mm., ponderosa pine 1.54 mm., Douglas fir 1.53 mm., sub-alpine fir 1.35 mm., and Engelmann spruce 1.30 mm. The increase per year for all trees during the century 1833 to 1932 was ponderosa pine 1.83 mm., lodgepole pine 1.81 mm., sub-alpine fir 1.54 mm., Engelmann spruce 1.41 mm., and Douglas fir 1.37 mm.

Water loss from atmometers ranked in the same order as water transpired from cut shoots. The ponderosa pine environment showed the greatest loss, the Douglas fir areas ranked second, the lodgepole pine third, and the lowest water loss was in the area of the Engelmann spruce.

According to potometer data, the lodgepole pine transpired the most, the ponderosa pine ranked second, and the Douglas fir transpired the least. These responses were modified according to the station environment indicated above.

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The relation between cell, nuclear and chromosome dimensions in a sterile violet species-hybrid¹

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(WITH PLATE 4 AND THREE TEXT-FIGURES)

In general it may be said that the data from the numerous investigations of chromosome numbers and sizes, in relation to hybridization potentialities and to the incidence of sterility and fertility, are conflicting. An analysis of older views which dealt with the problem of development from the point of view of cell interactions, i.e., rate and plane of cell division, is infrequent in current literature. The present writer feels that this method of approach perhaps might be a fruitful one. The study of Sinnott on *Acer* (1930) and of Sinnott and Kaiser (1934) on the morphological development of the fruits of *Cucumis* and *Cucurbita* are examples of this method of approach to the problem. The latter authors have secured highly interesting data on the growth rates at various stages of development, and have been able to correlate factors of cell growth with the emergence of fruit form.

In view of the comprehensive knowledge of chromosome number in the species of the genus *Viola* (Clausen, 1927, 1929, 1931; Gershoy, 1934) and the known relation of the number to species characters and potentiality of species hybridization, it seemed here advisable to attempt to relate chromosome number in the plants herein studied to the dimensions of the cells, nuclei, and chromosomes and to the amount of chromatin present in the nucleus. One purpose of the study was to determine the relation of such data to the problems of morphogenesis in species and species-hybrids.

In an effort to analyze the concept of the individuality of the chromosome, a portion of the study was devoted particularly to the careful measurement of somatic chromosomes in root tips. The direct bearing of this hypothesis upon the chromosome theory of heredity is obvious. Such supporting evidence as has been presented by Moenkhaus (1904), Baltzer (1909), and Tennent (1908), was concerned with the recognition of smaller and larger chromosomes in the hybrids. It would seem that in addition to such an approach, the theoretical importance of the problem requires a careful study of chromosome sizes in both parents and the hybrid. The apparent lack of a decisive difference in chromosome form in the genus *Viola*, between the small chromosomes making up a gametic

¹ Published with the approval of the Director of the Vermont Agricultural Experiment Station.

set (haploid-genom), leaves, as an alternative approach to this problem of individuality, the study of chromosome size.

The following observations embody the results of a statistical study of the characteristic cell, nuclear, and particularly the chromosome size relationships of the root tips of two species of *Viola* bearing unlike chromosome numbers, and the sterile species-hybrid derived therefrom. Cell size was investigated, in part to correlate if possible comparative size differences with nuclear and chromosome dimensions, and in part to compare with cell sizes of the mature tissue of the stem and leaf.

HISTORICAL

The literature pertaining to the individuality of the chromosome has been presented comprehensively in texts as, for example, Wilson (1925), and Sharp (1926, 1934). In general while the evidence is conflicting it may be said that most of it supports the theory rather than opposes it. As Wilson has pointed out, much of the evidence is very indirect, such as for example the constancy of chromosome numbers from one cell generation

Explanation of plate 4

Figures 1a, 3a, 5a, were drawn with the aid of a camera lucida, using a Zeiss 2 mm. apochromatic objective and a 20 \times compensating ocular. The projected magnification obtained was approximately 3100 \times . Each chromosome was numbered to facilitate counting and to permit accurate identification in measurement. Figures 1b, 2, 3b, 4, 5b, 6, represent photomicrographs taken with the aid of a Zeiss 2 mm. apochromatic objective and a 20 \times compensating ocular, on an Eastman process film, at approximately 1700 \times . The source of illumination was an improved Zeiss lamp, used with a prism reflector.

Fig. 1a. *V. papilionacea*, $2n=54$, inner periblem cell two cells outside of endodermis, from mature root tip.

Fig. 1b. *V. papilionacea*, $2n=54$, photomicrograph of cell drawn in figure 1a, at a smaller magnification.

Fig. 2. *V. papilionacea*, $2n=54$, photomicrograph of epidermal cell of mature root tip. Note that upper left corner of plate is out of focus.

Fig. 3a. *V. conspersa*, $2n=20$, inner periblem cell, one cell removed from the endodermis.

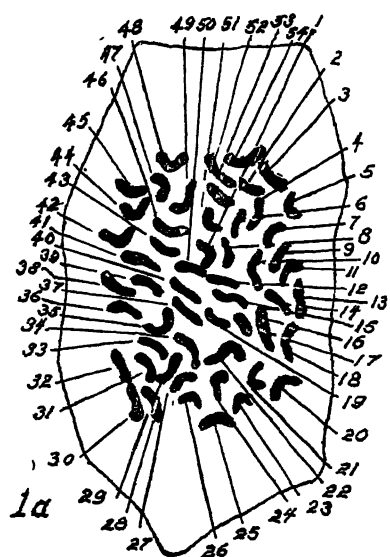
Fig. 3b. *V. conspersa*, $2n=20$, photomicrograph of cell drawn in figure 3a, at a smaller magnification.

Fig. 4. *V. conspersa*, $2n=20$, photomicrograph of cell located directly beneath the hypodermis.

Fig. 5a. *V. conspersa* \times *papilionacea*, $2n=37$, epidermal cell of mature root tip.

Fig. 5b. *V. conspersa* \times *papilionacea*, $2n=37$, photomicrograph of chromosomes drawn in figure 5a, at a smaller magnification.

Fig. 6. *V. conspersa* \times *papilionacea*, $2n=37$, photomicrograph of epidermal cell of mature root tip.



1b



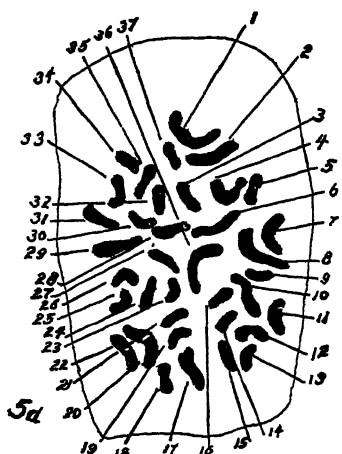
2



3b



4



5b



6

to another. Some investigators, however, have shown more definite data not only in constancy of chromosome number but in size and shape as well. The amount of work done on different genera, in which the karyotypes of the numerous species have been studied, is enormous.

Direct evidence for the persistent individuality of chromosome form, however, has been recently presented by McClintock on *Zea* (1931). This investigator, by demonstrating the presence of "genetic markers," has been able to trace discrete portions of chromosomes in various types of translocations and inversions, and to correlate such changes in chromosome form with genetic data. Her studies are being currently extended in investigations on corn and other genera.

Earlier data have been presented to demonstrate that there seems to be a persistence of the definitive chromosomes even through the resting stage of the nucleus. Richards (1917), using as material the eggs of *Fundulus*, has shown that the condensed chromosomes of the metaphase become vesiculated and that the nucleus is virtually made up of a group of separate elementary nuclei, or karyomeres, the boundaries of which though contiguous do not merge. Boveri (1909) had earlier demonstrated a somewhat similar condition in *Ascaris*, in which the nuclear lobes (representing chromosomes) present in the telophase reticulum, tended to assume the same relative positions in the following prophase. Although these lobes were similar in shape and position, they were confluent in the center of the nucleus. Kater (1928) indicates from his work on species of three different genera of plants that the reconstruction of daughter nuclei in somatic root tip tissue is accomplished by essentially the same process. The genera used were *Solanum*, *Lycopersicon*, and *Allium*, with chromosomes ranging in size from very small in *Solanum* to large in *Allium*. Although the drawings he presents do not show a persistent organization as clearly as do those of Richards, he suggests that chromosome vesiculation is probably the universal method of nuclear reconstruction.

Interesting data in confirmation of the individuality of the chromosome is that described by Wenrich (1916) for the grasshopper *Phrynotettix magnus*. In this insect certain chromosomes are individually recognizable by persistent characteristics of size, form and position of chromomeres, and behavior. After a careful study of the individual chromosomes during spermatogenesis, he concluded that the chromosomes retain their individuality and that each one possesses a definite organization which is expressed in the relative sizes and position of its chromomeres. He shows figures of one pair of prophase chromosomes in thirteen different individuals, all of which appear to be comparable. Though the concept of the existence of chromomeres as discrete portions of the chromosome has

been recently criticized, the method of carefully studying the individual chromosomes appears to be the best method of approach to the problem.

The theory of individuality has been attacked by various investigators. As Wilson states, Fick (1907) and Della Valle (1909, 1912) were among the first, the viewpoint of the latter having been presented by Wenrich. Della Valle likened chromosome formation to the formation of liquid crystals, and maintained that their identity was wholly lost in the resting nucleus. Wilson replies to the criticism that the chromosomes are temporary and variable structures, by asserting that it is a weakness to consider the chromosomes en masse, without further regard to their individual characteristics.

On the other hand, Morita (1927) finds a variation in number as well as in the size of chromosomes in the first spermatocyte of the orthopteran *Necrostethus grossus* (Linn.) and he concludes that it is difficult to harmonize his findings with the theory of chromosomal individuality.

Chamberlain (1925) from his studies of cycads concludes that both cytoplasm and chromatin are vacuolated and of essentially the same structure. "Definite chromomeres upon a linin ribbon afford a convenient resting place for genes, and facilitates philosophical speculation, especially if a theory demands a rigid serial arrangement of hereditary characters in the spireme. In a vacuolized chromosome there might be some serial arrangement, but it could not be so definite." Finally "he predicts that theories which cannot be reconciled with a vacuolated structure of the chromosome will have to be abandoned."

Avdulov and Titova (1933) in a study of additional chromosomes in *Paspalum stoloniferum*, showed that the heteroploid (23) chromosome individual possesses all the chromosomes of the normal set ($2n-20$) plus three small ones. Analysis of the morphological characters of plants with 20 and 23 chromosomes showed no difference of the phenotype. Hence the authors conclude that in their case the additional chromosomes seem to exert no influence on the phenotype. Furthermore, in some cases species notably akin morphologically differ sharply in their karyotype. The two to four surplus chromosomes lead to no essential changes in the structure of the corresponding organism. These authors avoided the apparent contradiction with the theory of localization of hereditary factors in chromosomes by regarding the additional chromosomes as vestigial. Yet the data secured in the recent work on extra-chromosomal types in *Datura*, by Sinnott, Houghtaling and Blakeslee (1934), demonstrate the influence of additional chromosomes on chromosomal balance and in turn on the anatomy of the mutants. Thus, the complexity of the relationship between

the presence of the additional chromosomes (and their contained genes) and the effect on the organism, is indicated.

Delage and Goldsmith (1919) in a general critique of mendelism, acknowledge the great advances in the field of genetic research, but think that there are many defects and uncertainties, and above all a fragility of the objective bases upon which mendelism rests. Their reasons for questioning the continuity of the chromosomes are: (1) They are not visible in the resting stage (in a few genera this may be questioned). (2) The linear arrangement of the genes is questioned because chemical differentiation within the individual chromosomes has not been demonstrated. (3) They contend that a force which will bring homologous chromosomes into such an intimate and accurate alignment as is necessitated by the chiasmotypy hypothesis will not permit them to lie cross-wise and give cross-overs. (4) They maintain that the mendelian conception gives no explanation of the successive appearance of characters in ontogeny, or of the origin of new characters in evolution. Finally they predict the collapse of mendelian concepts because of the weight of accessory hypothesis needed to explain special cases.

The work of Mathews (1924) would indicate that from a bio-chemical point of view the evidence is at best negative as regards any support for chemical differentiation in chromatin.

MATERIAL AND METHODS

Fixations. The root tips used were collected from plants grown in the greenhouse under conditions as nearly identical as possible. It was found that the plants were thriftier and produced better tips if they were transplanted and then allowed to grow in well aerated soil for several weeks. Care was taken to remove the surrounding soil from the roots by means of a gentle stream of water. Only the youngest and most healthy tips were selected for fixation, and these were from mature plants.

Two different killing fluids were employed: 1. La Cour's (1931), which he assumed to be especially adapted to root tip fixation, yielded fairly satisfactory results. 2. A modified S. Navashin solution² seemed to be the more satisfactory method at least with violet root tip material. Sections were cut eight to ten microns thick and stained in Heidenhain's iron alum-haematoxylin, care being taken to insure as uniform treatment as possible on the various sets of root tips.

² Developed in the cytology laboratory at this Station the proportions of fluids being as follows: To 180 cc. of Webber's modification of Navashin's fluid, 60 cc. of Flemming's medium solution was added to part A.

Cell Measurements. The method used in measuring cell areas of the dermatogen of the root was almost exactly the same as was used by Marvin (1936) in measuring areas of the cells of the stem and leaf. In each case 200 cells were drawn by means of a camera lucida at a magnification of 1500 times and the magnified drawings were measured with the planimeter. Longitudinal cell lengths were measured directly by means of an ocular micrometer at the same magnification as were the nuclear diameters.

Chromosome Measurements. All the chromosomes measured were first drawn with a camera lucida from carefully selected metaphase plates, at a projected magnification of 3100 diameters, with the aid of a Zeiss 2 mm. apochromatic objective and 20 \times compensating ocular. Higher magnifications, such as have been used by Navashin (1931) on *Crepis*, and by Lorbeer (1930) on *Sphaerocarpus*, entailed in the present case a distinct loss in clarity and definition of the outline of the chromosomes.

The measurements of the drawings were taken by means of a small strip of fairly heavy, pliable paper, carefully ruled in millimeters. The length of the middle axis of the chromosome drawing could thus be measured by means of this strip, despite the occurrence of curvatures in a horizontal plane. This simplified method was found to be quite effective. Navashin used a somewhat similar method but one which differed in the respect that his measurements were taken by means of dividers with the points set 3 mm. apart. He judged that he had attained by his method an accuracy of two to eight percent of the individual chromosome length (depending upon its total length) and two to five percent of the total length of the whole chromosome set.

It is evident that a source of error in measuring chromosome lengths may be due to a foreshortening caused by the curvature of a chromosome away from the horizontal plane. Navashin has criticized the projection method of Kagawa (1929). The latter attempts to reconstruct the actual chromosome length by a determination of the vertical distance involved in an upward or a downward curvature. Yet Navashin has pointed out that the measurement of vertical distances by means of the micrometer screw can hardly exceed an accuracy of less than one micron. Inasmuch as most of the vertical curvatures observed in the chromosomes here studied extended upward or downward only a fraction of a micron, it was thought best to disregard such curvatures when present. It seems, moreover, that in measuring chromosomes with several such curvatures the probable error would be high.

In the case of the violet roots careful focusing on the selected plates of the material used clearly indicates that some chromosomes show a

foreshortening, but that most of the chromosomes measured extended in a horizontal plane on the equatorial plate. This fact could also be verified by examining longitudinal sections of tips, in which the chromosomes were seen on the spindle from the side. At full metaphase not only are they apparently quite separate from each other, but in general they tend to lie in one plane. Such errors as result from the method of measurement employed doubtless give figures which are less than the actual values for the chromosome length because, where foreshortening has occurred, it has been disregarded for the reasons stated above. As can be seen from the photomicrograph of the chromosomes of *V. conspersa* (plate 4) their greater average length might show more of an error of this sort than the shorter chromosomes of *V. papilionacea*. Stated otherwise the error would be greater in longer chromosomes than in shorter ones. However, as Navashin has pointed out, since only relative values are required, a slight undervaluation of the actual length is permissible throughout.

The magnified chromosome lengths, recorded in millimeters, were transposed to their actual values in microns.

OBSERVATIONS AND DATA

Chromosome size in relation to cell and nuclear volume in the meristem of the root

The measurement of comparable cells in the root was undertaken to determine whether there exists on the one hand a constant cell size characteristic in any given tissue, and a correlation between cell volume and chromatin mass on the other. In order to measure cell volume two sets of measurements were necessary, i.e., (1) cross section areas and (2) longitudinal lengths of cells in the given tissue. The weighted mean area multiplied by the weighted mean cell height is a measure of cell volume. Obviously these two sets of measurements cannot be taken from the same root but must come from root tips which are as nearly comparable in size as possible. Although open to criticism for this reason, no other method seemed practicable in determining the volume of such cells.

As a measure of chromatin volume, both the total chromosome length of the diploid complement and the volume of the nucleus were used. It is apparent that in an estimate of nuclear volume the nuclear sap, the chromatin, and the achromatic substance are all included. It is likely that of the two methods the measurement of the total chromosome lengths alone gives a more accurate estimate of the amount of chromatin present in the nucleus. Of the two sets of data the greatest range of variation, from cell to cell, seemed to occur in the measure of total chromosome lengths.

Navashin (1931), whose earlier work dealt with a study of cell volume in relation to chromatin mass, measured total chromosome lengths alone. He has used this measure of chromatin volume without consideration of chromosome width, although admitting that widths between pure species may vary greatly. Furthermore, Navashin in his later paper (1934) states (page 196) that "great as this difference may be it disappears always whenever the chromosomes which display it are brought together in a hybrid cell." In the case of the material dealt with here the width of the chromosomes of *V. papilionacea* was less than the width of those of *V. conspersa*, while in the hybrid cells these initial differences still seemed to be apparent in the hybrid genom. It seems obvious, therefore, that while a measure of total chromosome length may serve as an estimate of the amount of chromatin, the chromosome width should not be disregarded.

I. Cell Measurements

Cross section areas. Bruun (1932) has recently re-emphasized that environmental factors probably operate less in the modification of the root tip meristem than in that of the shoot. For this reason, as well as the more obvious one that differentiation processes are practically absent, he considers the root tip meristem ideal to show a specific cell size. In examining a cross section of a violet root tip it is immediately apparent that not only does cell size vary appreciably from one tissue to another, but that it exhibits a wide range within a single tissue. In general, the parenchyma cells of the plerome tend, in any one cross section, to be smaller than those of the cortex or of the epidermis. The periblem displays the greatest variation in cell size, which ranges from the small innermost cells to the large cells of the hypodermal layer, which are the largest cells of the promeristem. The epidermis, which is made up of a single cell layer, contains cells of a size which is somewhat less than that of the hypodermis. Because the epidermis is but a single layer thick, and also because it shows a fairly narrow range in size variation as compared with the periblem, it is a favorable region for study.

Young (1933) measured carefully the cell lengths and breadths of five tissues of the apical three millimeters of corn roots. His observations showed that the transitional characters of each tissue could be observed separately. Each tissue seemed to have characteristics peculiar to itself as regards region of greatest division, time and speed of elongation, etc. Young favored the earlier view of Haberlandt (1914) that the three histogens of the root may in certain cases be traced to the common initial zone at the apex of the root.

The observations of the present writer made upon violet root tips,

considered in the light of Young's literature review, would seem to favor either Haberlandt's view, or perhaps would fall into the second class proposed by de Bary (1877) in which the plerome is sharply defined, but the periblem and dermatogen are united at the apex of the root. The position of the cross sections used in the present work lay in the upper half of the first millimeter and extended into the second millimeter. The exact distance from the tip was not determined as accurately as were those of Young, but the region was fairly defined by the number of sections from

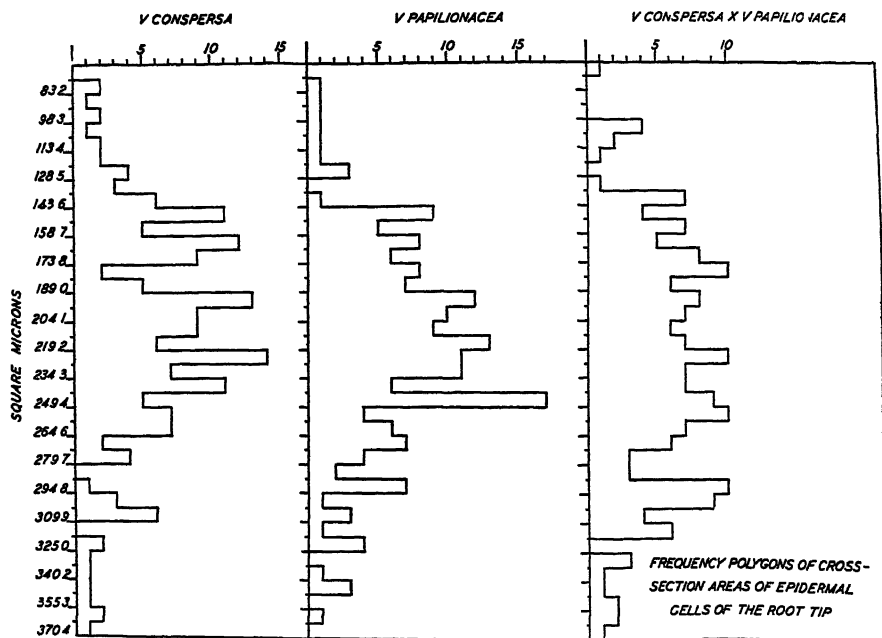


Fig. 1. Explanation in the text.

the tip. From similarly placed quadrants in serial cross sections, in an upward progression, strips including an average of ten adjacent cells were drawn in outline.

The data shown in the frequency polygons (fig. 1) are summarized in the following table (1). From the figures obtained it is apparent that there is present in the epidermis of the root of both species, a characteristic cell size. It also appears from the data that the mean cell size in the hybrid is intermediate.

From the figures presented in the table it may be observed that there exists a difference of approximately 12% between the mean cross section area of the epidermal cells of the parent species. Though the modal class shows figures of a somewhat higher value, there is almost an equivalent

difference, namely 10%. As can be seen from an examination of the graph, no definite modal class could be established in the measurements of the cells of the hybrid. However, the weighted mean cross section areas tabulated above seem to indicate that the area of the epidermal cells of the hybrid tends to be intermediate between the two parent species. It is to be noted further from the graph that the total range of cell areas, though rather wide in extent, seems to correspond very closely in the two species and the hybrid.

TABLE 1
Cross section areas of epidermal cells in square microns (see fig. 1)

PLANT	MEAN	MODE
<i>V. conspersa</i>	210.9	226.8
<i>V. papilionacea</i>	229.8	249.4
hybrid (C×P)	214.3	—

Longitudinal cell measurements. The measurements of epidermal cells shown in table 2 were taken from median longitudinal sections of root tips in the same region in which the cross section measurements were made (i.e., upper half of 1st millimeter, mainly in the 2nd millimeter). The length of a cell was measured on the axis of the cell parallel to the periclinal (longitudinal) axis of the root. The upper and lower transverse cell walls usually appear parallel to each other and perpendicular to the long axis of the root. Where one or both of these walls had been laid down at an oblique angle, the length on a line through the median, longitudinal central axis of the cell was recorded, thereby obtaining the average of the longest and shortest height.

Examination of table 2 showing the frequency distribution of cell lengths, indicates a rather wide range, varying from 6.6 to 22.8 microns. As less than one hundred measurements were taken from each parent and the hybrid, a well-defined modal class cannot be deduced from the table. A weighted mean, however, has been computed in each case from the measurements recorded, and is given at the bottom of the table. As in the case of the cross section areas there is again some evidence that in the hybrid there exists an intermediate expression, here shown in cell height.

It is of interest to note at this point a rather unusual method of cell elongation (stretching) which was apparent in a few tips cut in median longitudinal section. These particular roots indicate what seems to have been a periodicity in stretching of the cells of the epidermis, first along the radial and then along the vertical longitudinal axis of the cell. The expression of this periodicity or rhythm was such that four or five cells

would appear shortest along the radial or horizontal axis and at the same time longer along the vertical axis. Directly above this region, the cells would show an exactly reverse condition, the cells becoming wider and shorter. This gradual, alternate expansion along two different planes,

TABLE 2

Frequency distribution of the longitudinal measurements of the dermatogen cells of the root

MICRONS	PLANT		
	V. CONSPERSA	V. PAPILIONACEA	HYBRID C×P
6.6	1		
7.2	1		
7.8	1		1
8.4	8	1	3
9.0	4	2	1
9.6	18	0	2
10.2	2	1	6
10.8	9	5	7
11.4	0	0	4
12.0	12	4	13
12.6	1	1	3
13.2	2	4	4
13.8	3	1	3
14.4	2	5	4
15.0	2	4	6
15.6	4	3	5
16.2	1	1	1
16.8	2	7	1
17.4	0	2	1
18.0	2	9	3
18.6	0	3	1
19.2	1	4	1
19.8		2	0
20.4		5	2
21.0		3	0
21.6		1	1
22.2		0	
22.8		2	
Mean:	10.8	15.7	12.8

persisted back along the tip as far as the region of cell elongation. Freisner (1920) has shown a daily periodicity in cell division to occur in the root tip which may perhaps be reflected in the above configuration.

The observation made by Young (1933) that in the epidermis cell division was most active toward the upper half of the first millimeter rather than at the very apex, was observed to hold true in the present investigation.

II. Nuclear Measurements

TABLE 3

Nuclear measurements from cells of the epidermis showing frequency of distribution of diameters in microns

PLANT		FREQUENCY									
	MICRONS	6.6	7.2	7.8	8.4	9.0	9.6	10.2	10.8	11.4	12.0
<i>V. conspersa</i>		1	11	15	23	4	4				
<i>V. papilionacea</i>					3	12	11	13	18	13	1
hybrid, (C×P)			2	4	12	9	14	6	2		

Mean diameters = *conspersa* 8.1 μ ; *V. papilionacea* 10.1 μ ;

V. conspersa × *V. papilionacea* 9.0 μ .

The above figures are based on measurements of approximately fifty nuclei of each species taken directly from the stained sections with the aid of an ocular micrometer as had been done with the cell lengths. Though the majority of nuclei were spherical those which were elliptical in shape were measured on both their short and long axis and the average recorded. No fractions under one half a micron were included in the data. Due to the rather small range of size variation in the diameters measured, this number of measurements was considered to be fairly representative. As in the former sets of figures, the weighted mean was computed for each series. It is apparent that these mean nuclear diameters do not vary much from the modal class.

From the mean diameters given it can be seen that there is a percentage difference in nuclear size of approximately 20% between the two parents and that the mean diameter of the hybrid nuclei lies almost mid-intermediate between the two parents. That is, the hybrid nuclei seem to be ten percent larger than those of *V. conspersa*, and ten percent smaller than those of *V. papilionacea*.

III. Chromosome Measurements

The chromosome number of the two parents is quite different (*V. conspersa* 2n=20, *V. papilionacea* 2n=54) while the hybrid plants display a number (2n=37) which, as might be expected, is the sum of the haploid number from each parent species. Not only is there a rather marked difference in chromosome number between the two species, but there is also a very marked difference in chromosome size. Careful measurements of the somatic chromosomes were taken in both parents and the hybrid to determine if possible whether these characteristic size differences were truly persistent in the cells of the hybrid.

In view of the fact, recently emphasized anew by Navashin (1934), that chromosome size varies in different individual plants of the same species and probably from tissue to tissue of the same individual, it was considered essential to measure chromosomes that were comparable as regards their origin. Navashin (loc. cit) found that the chromosomes measured in mature roots displayed a range of size that was considerably larger than in embryonic roots. In a similar manner, Gershoy (1934) has observed that the chromosomes found in the vacuolated cells of the young flower bud tissue of different violet species show a tendency to be somewhat smaller than in the cells of the root tip. For this reason, therefore, the equatorial plates selected for measurement were all taken from: (1) mature roots; (2) in all but a few cases from the periblem of the root; (3) from the most actively dividing region just back of the growing point.

In spite of the precautions noted above, of selecting equatorial plates only from comparable regions of the root tip (as is noted in the graphs shown below of the classes of chromosome lengths in different cells of the same species) the range of size varies greatly from cell to cell. Even more significant is the fact that the individual sizes show an irregular distribution of lengths from cell to cell, an irregularity which in most cases is not even relatively comparable. To point out a striking example, in figure 2, curve III of *V. conspersa* shows eight chromosomes out of the diploid number of twenty ranging from 2.72μ to 3.84μ in length. In curve II directly beneath it, it is quite apparent that there are no chromosomes that equal in length even the shortest of the eight chromosomes which were present in curve III. In other words, none were longer than 2.5μ and most were considerably shorter. This is true in spite of the fact that the chromosomes were taken from cells which were in the same tissue of two tips which had been sectioned and stained simultaneously. The criticism might well be suggested that in spite of the similar treatment given to both tips, for some reason the chromosomes of curve II are simply more condensed than those of curve III. Yet even a glance at the two curves will show that they are not even *relatively* comparable whether in total range or in the different peaks shown. In fact a careful examination of the different curves (fig. 2) plotted for *V. conspersa* indicates that only two curves (I and II) seem at all comparable as regards the relative class distribution of chromosome lengths, and in both of these the range of size is quite different.

For a further analysis of these data curves II and III of the hybrid may be considered. It is to be noted that the curves were taken from periblem cells in both cases and that furthermore the curves are comparable as regards total range of chromosome lengths. Nevertheless,

curve III contained four chromosomes ranging in size from 1.92μ to 2.4μ whereas curve II showed no chromosomes in the same range of size. Apparently in the formation of chromosomes from the discontinuous spireme the chromatin condensed into smaller units or chromosomes about 1.28μ long, as is indicated by the peak at the left (II). It would seem that any attempt to identify all the members of the diploid complement from

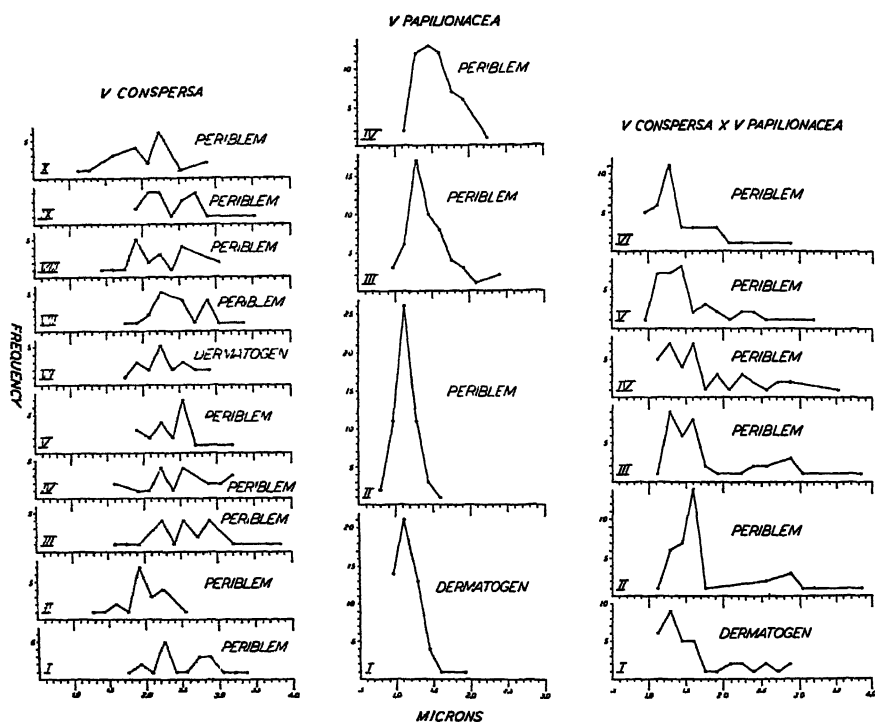


Fig. 2. Graphical curves showing the distribution of chromosome lengths of representative cells of the two parent species and the hybrid. (In each case the tissue from which the chromosome plate was drawn, is noted.)

cell to cell, on a basis of even comparable relative chromosome length, in this violet material at least, is extremely difficult.

The chromosomes from several cells of the epidermis have been measured to compare their sizes with those in the cells of the periblem. The curves shown on the chart indicate at least in the few cells measured, that chromosome sizes in the epidermis seem to be comparable to the smaller of the chromosome sizes found in the cells of the periblem. This would seem to agree with the observation made above (i.e., the epidermal cells appear to be smaller than the largest of the periblem cells). It should be

borne in mind, as pointed out above, that although the measurements plotted graphically are comparable, in some cases at least they are less than the actual chromosome lengths because of the foreshortening resulting from the position of the chromosomes on the equatorial plate. Any statement regarding the relation, if any, between cell size and chromosome sizes, would obviously require much more evidence.

The curves shown on the graph in figure 3 represent the frequency distribution of all chromosomes measured in the two species and the hybrid. A total of approximately 300 chromosomes were measured in each species,

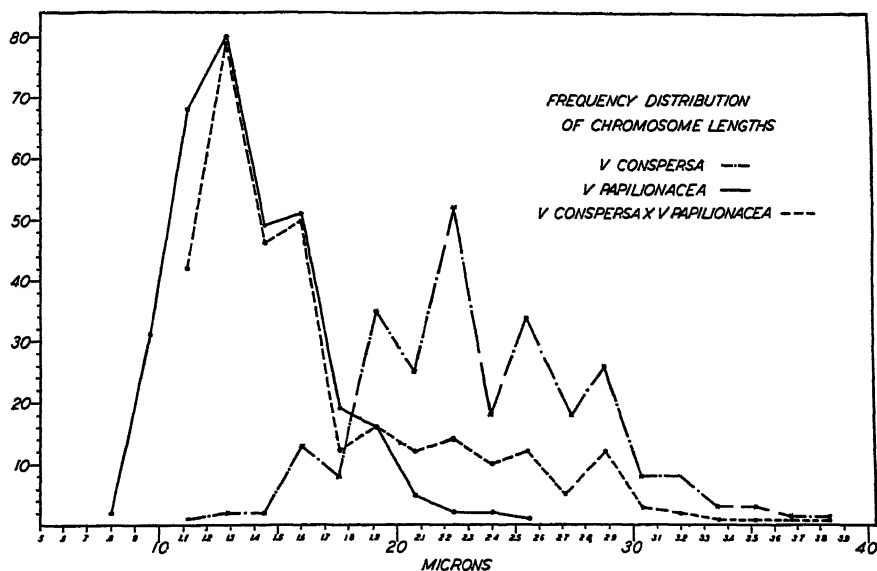


Fig. 3. Frequency distribution of total chromosome measurements taken in each species and the hybrid. (Approximately 300 in each case.)

a number which in a graphical curve obviously smooths out the individual difference noticeable in any single plate. It is apparent that the two parents each show fairly symmetrical curves of frequency distribution with a definite and characteristic peak, or modal class. The hybrid, on the other hand, shows a bimodal curve as regards the range of lengths with one modal class clearly defined and corresponding to modal class of the pollen parent *V. papilionacea*. Another peak, not as clearly defined, tends to be approximately $.3\mu$ smaller than the corresponding peak of the seed parent *V. conspersa*. Examination of the curve of *V. papilionacea* discloses the fact that 33 chromosomes of the genus (the first two points from left to right) are $.96\mu$ or less in length, while none of those measured in the hybrid cells were as small. In a comparison of the curve of the seed parent *V.*

conspersa with the curve of the hybrid it becomes apparent that if the longest of the hybrid chromosomes are as long as the longest of those of *V. conspersa*, the majority of them show a distinct tendency to be smaller. This apparent tendency for small chromosomes of the pollen parent to become larger and of larger chromosomes of the seed parent to become smaller in the hybrid cell is analogous to the condition found by Navashin in some of the hybrids between species of *Crepis*, which had different chromosome sizes in either parent. He has given the term neutral amphiplasty to this neutral, reciprocal influence in the hybrid in which the whole chromosome complement of either parent seems to be affected under the new conditions which obtain in the hybrid cell.

TABLE 4

Differences between the absolute total lengths of the diploid chromosome sets of the two parent species and their hybrid. From adult roots (compare with fig. 2).

PLANT	PLATE NO.	MICRONS	
<i>V. conspersa</i> (2n=20)	I	49.0	
	II	39.3	
	III	51.2	
	IV	50.6	
	V	47.9	Min.—39.3
	VI	46.9	Ave.—46.9
	VII	50.3	Max.—50.6
	VIII	44.3	
	IX	48.8	
	X	41.1	
<i>V. papilionacea</i> (2n=54)	I	63.3	Min.—61.7
	II	61.7	Ave.—71.9
	III	78.5	Max.—84.1
	IV	84.1	
<i>V. conspersa</i> × <i>V. papilionacea</i> (2n=37)	I	61.7	
	II	67.5	
	III	67.7	Min.—54.6
	IV	65.6	Ave.—62.6
	V	59.1	Max.—67.7
	VI	54.6	

(In the above table the figures opposite the Roman numerals merely represent the summation of the measurements of the chromosomes from that particular equatorial plate. The Roman numerals refer directly to the frequency curves plotted on the graph of figure 2.)

A tabulation of the total chromosome lengths in several cell plates, given in table IV, is of interest. It is to be noticed that there exists here, as in other measurements, a rather wide range of total chromosome lengths

from cell to cell, least in the hybrid and greatest in *V. papilionacea*. The computed average, underlined in the table, indicate a fairly close correlation with another possible measure of chromatin mass, namely nuclear volume. Furthermore, there is also a correlation on the one hand between chromatin volume measured by both methods and chromosome number, and cell volume on the other.

TABLE 5

SPECIES	CELL				NUCLEUS		N/c RATIO
	RANGE	CROSS SEC- TION AREA SQ. MICRA	LONGITUD. DIMENS. MICRA	COMPUTED CELL VOL. CU. MICRA	DIAMETER MICRA	COMPUTED NUC. VOL. CU. MICRA	
<i>V. conspersa</i>	Min.	83.2	6.3		6.6		
	Mean	210.9	10.8	2277.7	8.1	268.1	1:7.4
	Max.	370.4	19.2		9.6		
<i>V. papilionacea</i>	Min.	83.2	8.4		8.4		
	Mean	229.8	15.7	3607.8	10.1	523.6	1:5.8
	Max.	423.3	22.8		12.0		
Hybrid	Min.	75.6	7.2		7.2		
	Mean	214.3	12.8	2743.0	8.6	333.0	1:7.2
	Max.	370.4	21.6		10.8		

The above composite table presents at a glance the cardinal points in the range of the cell and nuclear measurements taken. It also shows the computed cell and nuclear volumes for the cells of the epidermis of the two parent species and the hybrid, as well as the nucleo-cytoplasmic ratios computed from the mean cell and nuclear volumes. These compare very closely with ratios given by Klieneberger (1918) for tissue of the root tip meristem of different genera.

DISCUSSION

An analysis of the above data, in the light of the current literature, touches upon several problems of theoretical interest. It seems that the karyotype is not fixed and unvarying in form, but rather as Navashin (1934) and others have shown [Delaunay (1931), Kagawa (1929)] that it is subject to environmental as well as to inherent alterations occurring in the ontogeny of an organism. Aware of this fact, the writer has taken precautions mentioned above, to select root tips grown under uniform conditions as well as to subject them to a similar treatment in preparation for staining. The measurements of chromosome plates were taken from cells which were in most cases from comparable regions of the same tissue of the root.

The following question at once presents itself: is the occurrence of marked differences in total chromosome lengths and the even more, apparently, fortuitous distribution of individual chromosome lengths from cell to cell compatible with the theory of chromosome individuality in the sense of genic and chromomeric make-up? In spite of the rather marked differences in total range as well as distribution of chromosome lengths in comparable cells of the same species, a comparison of approximately 300 chromosomes from each parent and the hybrid shows that there has occurred an alteration in the hybrid, at least as regards the chromosome lengths of its parental haploid complements. This condition noted in the chromosomes of the hybrid cells, called "neutral amphiplasty" by Navashin, seems to indicate that the hybrid consists of cells and formed cytoplasmic components which, together with its chromosomes, are not characteristic of either parent alone but rather of the hybrid organism. There is suggested the occurrence of an interaction of two different protoplasts, from fertilization to physiological maturity. A preliminary study of flower buds produced late this year indicates that not only is the flower bud formation delayed, but that the maturation divisions in all but a few buds do not progress beyond the prophase of the first division.³ Bold and Gershoy (1934) have pointed out in connection with studies made on other sterile species hybrids, that despite the apparent vigor of the hybrid organism the disturbed cell and nuclear relations are not limited to the spore tissue alone but are indicated elsewhere by the almost complete breakdown in differentiating tissue which may occur at various stages of flower bud formation, and usually previous to the maturation division in sporogenous tissue. It is here suggested that when statistically considered, the apparently haphazard size-distribution of the individual chromosomes of a complement from cell to cell in the same tissue of a given species, would probably be found to be the normal condition if a sufficiently large number of measurements were taken.

Even a cursory analysis of the literature regarding the importance of the individuality of form and size of the chromosomes, in relation to the expression of a definite morphology in the organism, reveals conflicting points of view. Navashin (1934), in discussing the views of earlier authors, quotes Morgan, Sturtevant, and Bridges, who say that "not the shapes and sizes of the chromosomes" are important "but the genes contained

³ Subsequent studies of more fully developed flower buds showed complete asynapsis, along with the highly abnormal meiotic divisions characteristic of this type of sterile, violet species-hybrid. Such erratic and abortive reduction divisions in other sterile species-hybrids have been described earlier (Bamford and Gershoy, 1930; Bold and Gershoy, 1934).

in them." Yet, as Navashin points out, "this formula . . . cannot satisfy because the 'unimportant' sizes and shapes of the chromosomes are the only so far visible characteristics of the carriers of the genes" . . . "we would never guess the existence of genes unless we observed their developmental characteristics." He stresses the fact, moreover, that these characteristics can only be inferred from the chromosomes as we see them. It would seem to follow that a high degree of constancy in shape and size is necessary for the validity of the gene theory.

The conclusion of Navashin that the chromosomes are not "absolute things" but are rather influenced somewhat by the surrounding cellular medium is apparently borne out by the present investigation. Navashin, however, apparently does not consider the variation in chromosome sizes, which he has found, to be of such a magnitude as to conflict with the general idea of chromosome individuality. Yet the present writer is of the opinion that if evidence is presented for the occurrence of neutral amphiplasty and the presence of an appreciable range in variation in chromosome size from tissue to tissue, or even within the same tissue, the data should show that the variability is at least comparable. That the measurements here presented do not show evidence for the existence of even comparable variation in the distribution of chromosome length from cell to cell, particularly in the periblem of the root meristem, is quite obvious and significant. The data suggest rather that the chromatin of the nucleus, in its normally recurring cycle of condensation, accompanying the formation of chromosomes as discrete units and alternating with the diffusion and redistribution in the so-called metabolic phase, reappears as units which may express in somewhat haphazard fashion the same size-and-form range.

The evidence for the existence of a definite and constant chromosome individuality, similar to that found by Wenrich in the chromosomes of *Phrynotettix*, seems rather scanty (Sharp, 1934). In the diploid hybrid genom here studied there is no complete retention of the size characteristics of the haploid sets of the parents nor do they show a complete merging of size characteristics, as might perhaps be expected. Although the longer chromosomes of *V. conspersa* tend to become shorter and the shorter chromosomes of *V. papilionacea* parent tend to become longer in the hybrid, the chromatins of the two parents nevertheless do display an individuality of organization as species characters, expressed in the range of distribution in chromosome length, characters which are not entirely lost in those chromosomes which make up the hybrid genom. It may of course be possible but rather difficult to show in most species that the chromosomes never lose their individuality even in the resting phase, but

do become vesiculated as various investigators mentioned above have postulated. The evidence for the maintenance of chromosome individuality in the form of vesicles exists only in scattered instances. But the inference is still current that an individuality of some sort persists from one division to another.

A much simpler hypothesis might perhaps be advanced, namely, that a very slight difference in chemical composition of the chromatin of either parent would tend to keep the two separate, thus accounting in the hybrid genom for the persistence of species characteristics.

From the data presented here and by Marvin (1936), and from the evidence brought forth in the literature on the problem, the direct relation of cell size to morphogenesis is not clearly established. Less tangible is the bearing of the nucleo-cytoplasmic ratio on form development in the many celled organism. That the size and form of the chromosomes as such, are directly concerned with differences in morphological expression, is by no means established, although the indirect evidence secured from the vast data of genetical studies definitely assumes such a direct relationship.

The data, in the violets at least, indicate that a more intensive biometric study of the normal range of variation in chromosome size and shape is a necessary prerequisite of one critical approach to the fundamental validity of current cyto-genetical assumptions.

This study was carried on under the direction of Dr. A. Gershoy, to whom I am indebted for many helpful suggestions and criticism as well as for the use of his pedigreed stock. In addition I wish to express my gratitude to Professors G. P. Burns, B. F. Lutman, and R. A. Harper for criticism of the manuscript.

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An abnormal method of branching

P. A. DAVIES

(WITH PLATE 5 AND TWO TEXT-FIGURES)

An abnormal method of branching occurs at the apex of many rapidly growing shoots of *Ailanthus altissima* Swingle. The writer, during the past three seasons (1932-1934), has found 204 cases of this method of branching. It is so unusual and so different from the normal method of branching that its structure and ontogeny is of interest.

The normal method of branching in *Ailanthus* is forked and irregular, with shoots developing at irregular intervals along the mother shoot (pl. 5, fig. A). The large pithy area in the center of the mother shoot is not continuous with the pith of the branch; an intervening area is occupied by the wood (pl. 5, fig. B). The abnormal method of branching, which appears at the apex of the mother shoot, is fan-shaped and flattened (pl. 5, figs. C and D). The pith of the mother shoot is continuous with the pith of the branches and no intervening areas of wood appear.

Shoots in the normal method of branching arise from buds which developed the previous season. These buds form in the axils of the leaves, so the position of the leaves on the stem determines the position of the new shoots. If all the buds developed into shoots, the shoot arrangement on the mother stem would be as symmetrical as the leaf arrangement; but not all the buds develop, so the branching presents an irregular pattern.

Theiss,¹ studying 661 mother stems of *Ailanthus*, found that the number of shoots on a stem varied from 1 to 8, with an average of 2.24. The abnormal method of branching occurs at the apex of rapidly growing shoots, and its growth and position are not dependent on bud formations of the previous seasons, but is the result of an abnormal distribution of leaves on the shoot of the current season's growth. The position of the shoots in both the normal and the abnormal methods of branching depend on leaf position; the normal on leaf position of the previous season's growth and the abnormal method on leaf position of the current season's growth. An understanding of leaf position is important in understanding the cause of this peculiar method of branching. The normal leaf arrangement or system in *Ailanthus* is octostichous or eight-ranked. The angular divergence of the leaves is 135° or three-eighths of a circumference. In such an arrangement, with the completion of the third revolution, leaf number nine is in position in line with leaf number one. Wright (1867) points out that in this type of arrangement the leaves are distributed

¹ Theiss, E. W. 1933. Factors affecting the method of branching in *Ailanthus altissima*. Unpublished thesis. Univ. of Louisville.

most thoroughly around the stem, exposed most completely to light and air, and provided with the greatest freedom of symmetrical expansion, together with a compact arrangement in the bud. The regular distribution maintains the normal symmetry of the stem. In the abnormal method of branching, the lower part of the mother shoot has the normal three-eighths leaf arrangement and the normal symmetry. At the apex of the mother shoot, the normal leaf arrangement is destroyed and the leaves appear in an abnormal arrangement (pl. 5, figs. C and D). With the completion of the third revolution, leaf number nine is not in line with leaf number one. When the symmetry of the shoot has been destroyed to such an extent that it flattens at the apex, the peculiar method of branching appears.

In any season, the normal shoot growth in *Ailanthus* is of two types: (1) short spur-like shoots (pl. 5, fig. A), which are rarely more than eighteen inches long; and (2) long shoots, which may reach more than sixteen feet in length. The spur-like shoots are found on older trees, which because of extension growth, produce many but short shoots. The spur-like shoots on the upper part of the tree generally terminate in flower panicles. The long shoots on young rapidly growing trees, which produce few shoots, often only one, never terminate in flower panicles. The spur-like shoots (slow-growing shoots), as far as observations have been able to determine, produce only the normal leaf arrangement and the normal symmetry. In the long shoots (rapidly growing shoots) the normal leaf arrangement at the apex is the rule, but exceptions in the form of abnormal leaf arrangements occur, which may result in a flattened stem.

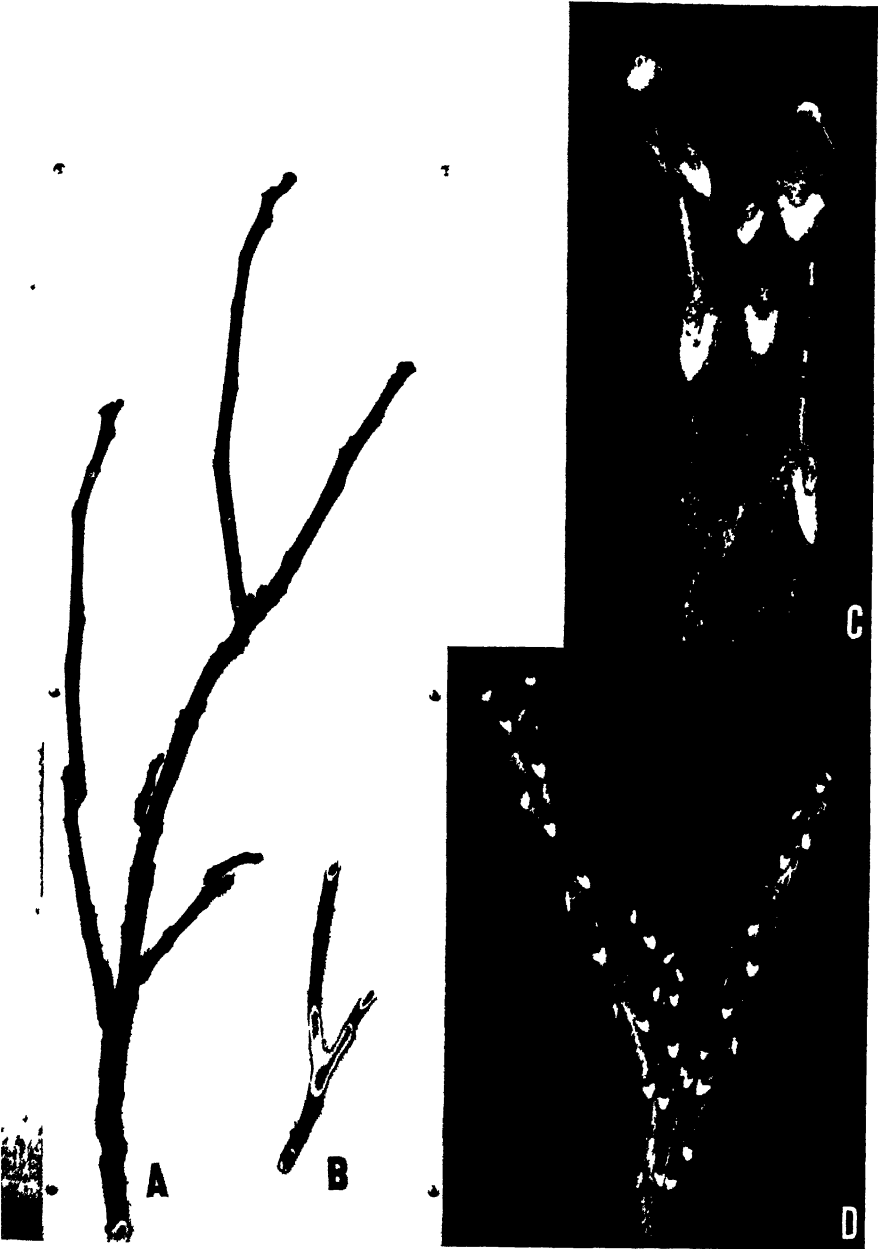
As the abnormal method of branching is found at the apex of rapidly growing shoots, and as it is the result of an abnormal arrangement of leaves on the shoot, it appears that rapidity of growth is an internal correlatory factor in determining the position of the leaf primordia at the rapidly differentiating shoot apex in *Ailanthus altissima*. Evidence is at hand to support the statement that internal forces play a rôle in determining leaf position. Winkler (1901, 1902) states that inner correlations along with heredity and outside influences determine leaf arrangement,

Explanation of plate 5

Fig. A. A tip of one of the main branches of a large tree. The method of branching is forked and irregular.

Fig. B. Normal branch with part of the wood cut away so as to show the union between the branch and the mother stem. The pith of the branch is not continuous with the mother stem.

Figs. C-D. Apices of rapidly growing young shoots which have flattened and are in the process of branching. Distinct growing centers may be observed. Leaf scars indicate the position of the leaves.



DAVIES ABNORMAL BRANCHING

and that no single factor plays an important rôle in all types of leaf arrangement. Schwendener (1901) states that pure mechanical causes (internal forces) acting at the place of origin determine leaf arrangement.

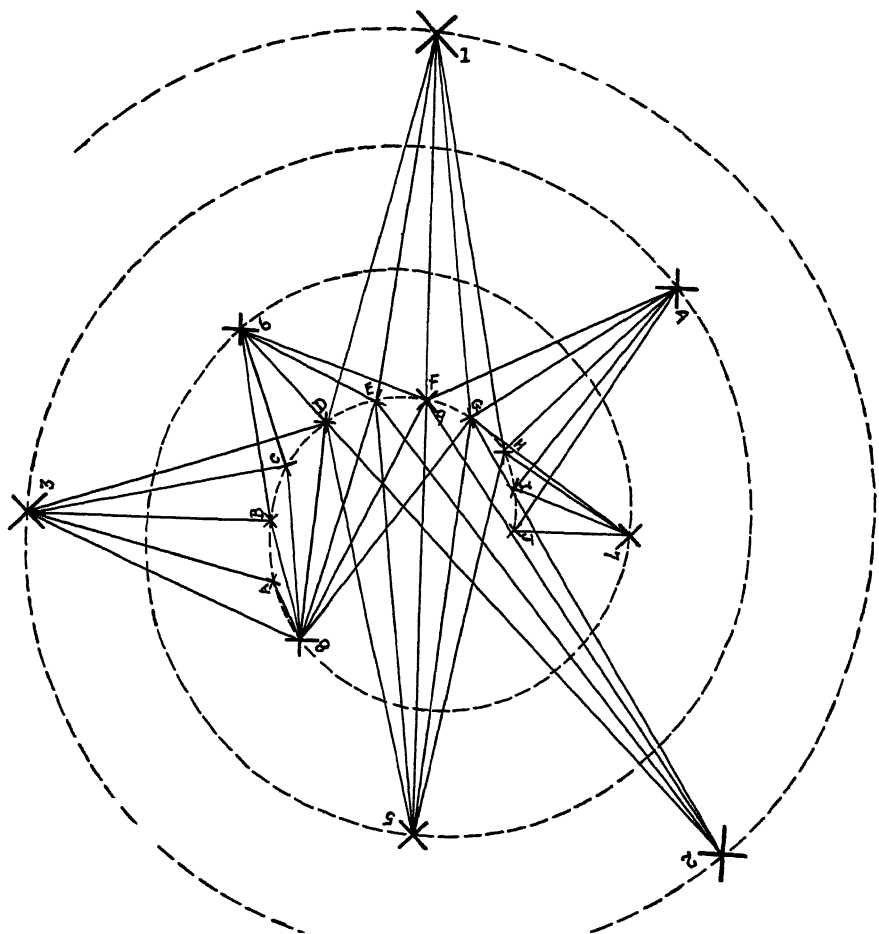


Fig. 1. A diagrammatic representation of a complete cycle in the normal three-eighths leaf arrangement. Crosses marked 1, 2, 3, 4, etc., represent developing leaf primordia. Crosses marked A, B, C, D, etc., are assumed positions of leaf primordia. The straight lines drawn from the developing leaf primordia to the assumed primordial positions represent the extent of influence the developing leaf primordia have over the assumed primordia. The shorter the line the greater the influence.

Foster (1928) says that evidence at hand suggests that the leaf primordia at the growing apex are genetically multipotent and hence capable of developing along a number of lines which are secondarily determined by

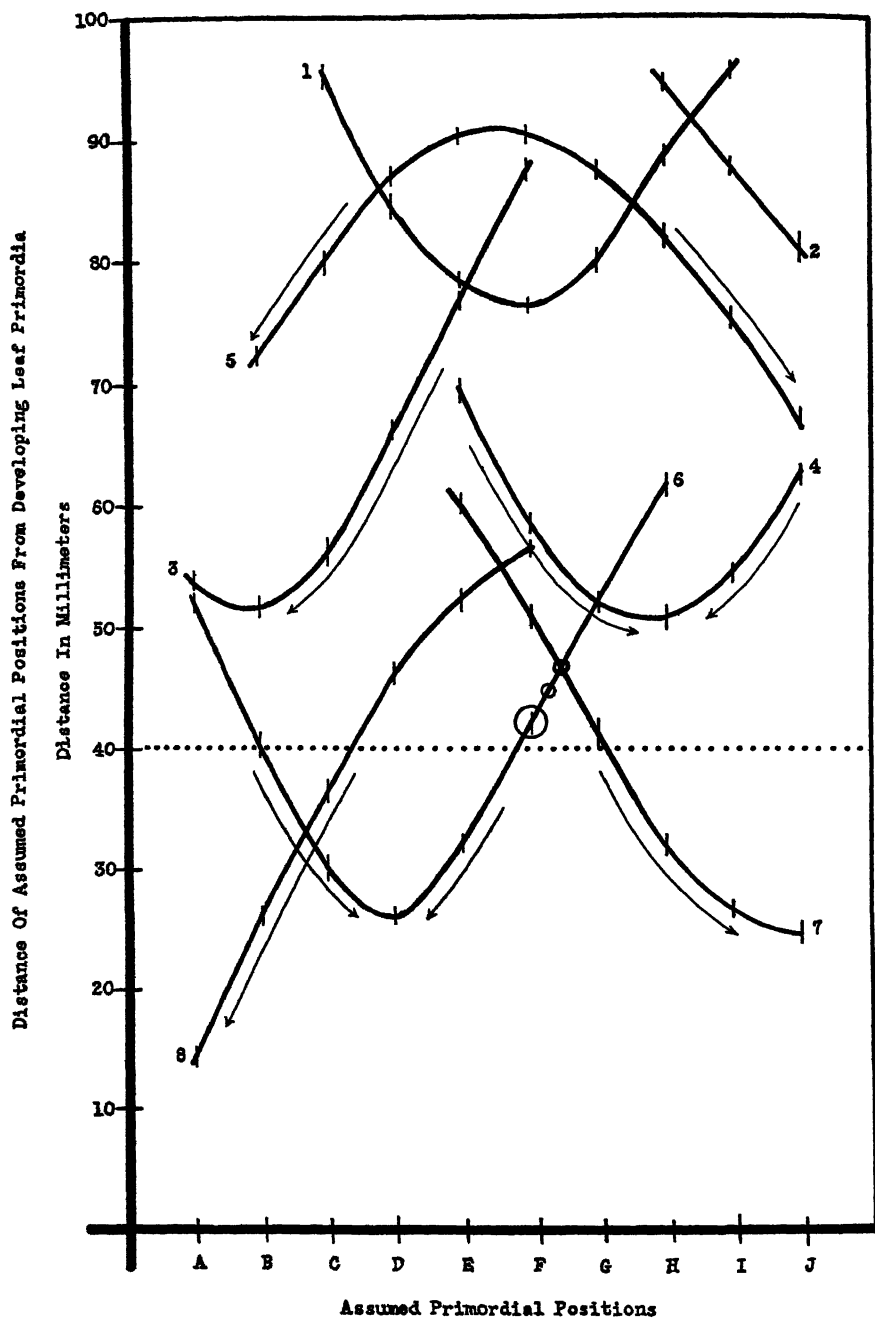


Fig. 2. A graphic representation of the data given in fig. 1. Each curve represents the influence that a developing leaf primordium has on the assumed primordia. The arrows indicate the direction of increasing influence. The large circle indicates the position of the developing normal ninth leaf primordium relative to the extent of influence exerted by the developing leaf primordia.

external and internal forces, and the relation of the growth initial to the shoot as a whole.

Figure 1 is a schematic arrangement which illustrates the relative position of the leaf primordia in a complete cycle in the normal three-eighths leaf arrangement. The spiral is viewed from the apex of the shoot. The leaf primordia in the outer part of the spiral are older. Leaf primordium 1 is the oldest and farthest down the shoot, while leaf primordium 9, at the apex, is the last one formed. Crosses marked A,B,C, D,E,F, etc., are assumed positions where leaf primordia might develop from the undifferentiated tissue at the apex of the shoot. Assumed leaf primordial position F is the position of the primordium which normally develops into the ninth leaf and completes the cycle. The lengths of the straight lines drawn from the developing primordia to the assumed primordial positions represent the extent of influence (dominance) that the developing leaf primordia have on the undifferentiated tissue at the apex of the shoot. The shorter the line the greater the influence.

Figure 2 shows a graphic representation of the data given in figure 1. Each curve represents the dominance, indicated by the length of the lines in figure 1, that a developing leaf primordium has on the assumed leaf primordia. The arrows indicate the direction of the greatest influence. The large circle indicates the position (assumed position F) of the normal ninth leaf primordium relative to the extent of influence exerted by the developing leaf primordia. The dotted line indicates the extent of the dominating influences of the leaf primordia on the assumed primordial positions. Below the dotted line, the dominating influence is great enough to prevent the development of a leaf primordium in the assumed positions; while above the dotted line, the influence is not great enough to prevent the development of leaf primordia in the assumed positions. The influence of leaf primordium 8 is sufficient to prevent the development of a new one in assumed position A. The combined influence of 8 and 6 is sufficient to prevent new ones from developing in assumed positions B and C. The influence of 6 is sufficient to prevent the development in assumed position D and E, but the influence is greater at D than at E. At the assumed position F, just above the dotted line, the position at which the normal ninth leaf develops, the influence of combined existing leaf primordia is not great enough to prevent the development of a normal leaf primordium in this position. The newly formed ninth leaf primordium matures to such an extent that it exerts a dominating influence sufficient to prevent the formation of a new one in assumed position G. The combined influence of 9, 7, and 4 is sufficient to prevent the formation of primordia in assumed positions H, I, and J. Not until a position is reached, above leaf pri-

mordium 2, where a decrease of influence similar to that exerted at position F, will another normal leaf primordium develop. In the abnormal method of branching, growth is so rapid at the apex of the shoot that additional leaf primordia (indicated by the small circles) are formed in close proximity to the ninth leaf primordium before it can mature sufficiently to exert an influence preventing the development of additional leaf primordia. Multiple development may continue until the influence of leaf primordium 7 or the cessation of rapid growth so that the last formed primordium can mature sufficiently to exert a controlling influence, stopping the multiple development. Another one will not be formed until a position is reached where the lowering of the influence is sufficient to allow a new leaf primordium to develop, and this new one will be out of normal position. When they develop out of the normal position, they destroy the normal symmetrical leaf arrangement above that point. The abnormal arrangement of leaves results in an unequal demand for conducting tissues. If the leaves occur in opposite groups on the shoot, opposite increases of conducting tissues will result. This opposite growth will result in a flattened shoot. If the shoot becomes very flat toward the apex, the intervening areas between the growing centers split. The separating of the growing centers result in the abnormal method of branching.

SUMMARY

An abnormal method of branching occurs at the apex of many rapidly growing shoots of *Ailanthus altissima*.

An abnormal distribution of leaves occurs. This results in a flattened stem apex with definite growing centers. The intervening areas between the growing centers split, resulting in the abnormal branching pattern.

An explanation of the process is given.

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New and noteworthy trees in Texas and Mexico

C. H. MUELLER

In July, 1933 an elm lacking fruits was collected and repeatedly observed in the Sierra Madre Oriental in Diente Canyon about twelve miles south of Monterrey, N. L., Mexico. It was found commonly scattered in two deep, moist, and wooded arroyos ranging from 3,000 to 5,000 feet in altitude where it grows in association with *Tilia*, *Cercis*, and several oaks.

The vegetative characters very strongly suggest *Ulmus americana* L. to which it is apparently closely related. Standley writes,¹ "Sessé and Mociño reported (Pl. Hisp. 45. 1887) *Ulmus americana* from Mexico. The plant (if the report is based on an actual plant) probably belongs to some other genus." It seems reasonable to believe that Sessé and Mociño might have encountered in vegetative condition the species here described as new, for it was not until the collection of fruits in May, 1934 that critical characters distinguishing it from *U. americana* could be recognized beyond doubt.

The collection of fruits was not accomplished without difficulty, for the time of fruiting is evidently in very early spring, and hardly any but fallen fruits and peduncles which were lodged in debris-filled crevices could be found. That these were not dropped the autumn before was clearly indicated by the occasional finding of fruits lodged in comparatively fresh and fragile spider webs which could hardly have survived the winter intact in their unprotected situations.

The species differs from *U. floridana* Chapm. in its bristle-clothed leaves and short petioles. It may be distinguished from *U. alata* Michx. by its merely ciliate samara wings and hispidulous leaves. It differs from *U. fulva* Michx. in its ovate samara with the wings glabrous save for the ciliate edges. From *U. americana*, to which it is closely related, it differs in having the tips of the samara widely divergent and quite indurated. Mr. Paul C. Standley, to whom some vegetative specimens were submitted suggested the possibility that the species might prove distinct if the fruits were known. The character of the persistent styles or samara tips suggests the name *Ulmus divaricata*. A description follows:

Ulmus divaricata C. H. Muell. sp. nov.

A small tree usually about 10 m. tall with a trunk diameter of 30 cm. or less and moderately but rather finely furrowed, dark brown bark in thin,

¹ Contr. U. S. Nat. Herb. 23: 198. Standley credits only *U. crassifolia* Nutt. to Mexico and that by the inference that it must cross the Rio Grande from the Texas border country where it is common.

narrow plates. Branches long and gracefully spreading. Twigs round, very slender (0.6 to 2 mm.), reddish brown, rather densely pubescent with short, silky hairs, becoming glabrous during the second year and acquiring a few light gray, rather inconspicuous lenticels (or light brown, conspicuous ones in the case of very vigorous shoots). Buds brown, conical, decidedly acute, about 1×2 –2.5 mm. with a pair of awl-like stipules about 5 mm. long usually persistent. Leaves broadly lanceolate to sub-ovate, twice serrate with acute, somewhat mucronate, incurved teeth, inequilaterally somewhat auriculate at the base, moderately small (1 – 3.5×3.5 –8 cm.) or on vigorous shoots broader, long attenuate at the apex, narrow at the base, and moderately large (as large as 7×14 cm.); the two surfaces roughened by very stiff, short hairs sparsely distributed and not readily visible; midrib and veins slightly impressed above and prominent beneath with short, dense, silky hairs; petiole short (0.5 – 1.5×2 –5 mm. depending on the leaf size), brown, and densely soft-pubescent like the midrib. Flowers vernal (by inference). Fruiting peduncles 20–25 mm. long bearing 5–8 pedicels 6–8 mm. long which bear thickened nodes well above the middle as though there might earlier have been bractlets. Fruit falling from the pedicel before the deciduous peduncle; samara ovate to obovate, about 3 – 5×5 –8 mm., deeply notched at the apex, the styles broadly divergent or rarely merely erect, 1–1.5 mm. long, indurated and usually finely tapered; the wings margined by a heavy vein, glabrous except for being densely ciliate strictly on the edges. (Not every specimen exhibits this character plainly; on some the hairs are extremely short, and on others apparently the material has been somewhat damaged by exposure to the weather. It is quite distinct on most of the better preserved specimens, however.)

Ramuli graciles, annotini dense breviterque pubescentes; gemmae conicae acutae, circiter 2–2.5 mm. longae 1 mm. crassae, stipulis subulatis circiter 5 mm. longis plerumque persistentibus; folia ex late lanceolatis fere ovata, 3.5–8 cm. longa, 1–3.5 mm. lata, duplo serrata, basi inaequaliter subauriculata, utrinque pilis brevibus rigidis asperata, venis supra impressis, subtus prominentibus pilis brevibus confertis sericeis; flores vernaes; pedunculi fructiferi 20–25 mm. longi; pedicelli 5–8, 6–8 mm. longi, ultra medium nodosi locum bractearum indicantes; samarae ex ovatis obovatae, circiter 5–8 mm. longae 3–5 mm. latae, apice alte retusae, stylis induratis late divergentibus aut rare erectis; alis glabris marginibus dense ciliatis exceptis.

The types [C. H. & M. T. Mueller no. 62 (vegetative) collected July 4, 1933 and no. 251 (fruit from the same individual tree) collected May 6, 1934, in Diente Canyon about 12 miles south of Monterrey, N. L., Mexico] are deposited in the herbarium of the Arnold Arboretum at Jamaica Plain, Mass., and in the author's herbarium at Cuero, Texas. The herbarium of the New York Botanical Garden contains a co-type. The herbaria of the Field Museum of Natural History at Chicago and the University of Texas at Austin contain vegetative specimens of which no. 61–1933 is atypical

in that it consists of vigorous shade branchlets with abnormally large leaves.

In a collection of plants made in July and August, 1933 in and about Diente Canyon of the Sierra Madre Oriental about twelve miles south of Monterrey, Nuevo Leon, Mexico, by the author and Mary Taylor Mueller there were found ten species and eight forms of oaks. Of these five species and two forms have been identified as follows by Dr. Wm. Trelease and the author: *Quercus polymorpha* Cham. & Schl., *Q. fusiformis* Small, *Q. Muehlenbergii* f. *Alexanderi* (Britton) Trel. (?), *Q. Standleyi* Trel., *Q. rysophylla* Weatherby, *Q. Canbyi* Trel., and *Q. Canbyi* f. *adscendens* Trel. The form here referred to *Q. Muehlenbergii* f. *Alexanderi*, although it may not quite fit the form, represents a considerable though not unexpected extension of the range of the species. *Q. Muehlenbergii* Engelm. is found in the mountains of western Texas and New Mexico.² *Q. Standleyi* was known previously only from the Sierra Madre Occidental.³ This collection adds considerably to its range. The remaining forms could not be placed critically and are here described as new.

A more recent collection in more southerly localities of the Sierra Madre Oriental promises to yield many additional facts of distribution and relationships of some of these species. This collection will be described later as time permits.

The types of the species described below are deposited in the herbarium of the University of Illinois at Urbana. Series of co-types (named in the order of completeness) are preserved in the Mueller Herbarium at Cuero, Texas, the herbarium of the University of Texas at Austin, and the herbarium of the University of Mexico in Mexico City.

***Quercus clivicola* Trel. & Muell. sp. nov.**
(*Leucobalanus*—*Glaucoideae*)

Twigs rather slender (2–3 mm.), somewhat fluted, rusty-tomentulose for a time, becoming gray with rather conspicuous lenticels. Buds globose and gray becoming ovoid and 2×3 mm., the upper accompanied by long setaceous stipules. Leaves elliptic-oblong, broadly acute or sometimes obtuse, cordate, entire or somewhat undulate upwards, narrowly revolute, 2–4×6–11 cm., dull, glabrous and minutely cancellate above, yellowish-subtomentulose beneath; veins some 10 or 12×2, looping; petiole tomentulose, scarcely 5 mm long. Staminate catkins about 40 mm. long, loosely flowered, the pistillate about 45 mm. long in summer with flowers apparently sessile and paired or in threes. Fruit annual, finally solitary or paired in groups on the tomentulose

² Wootton and Standley, Contr. U. S. Nat. Herb. 19: 171.

³ Trelease, Mem. Nat. Acad. Sci. 20: 57.

peduncle; cups deeply saucer-shaped, 15 mm. or more in diameter, with obscurely keeled acute appressed scales gray or brown when glabrate; acorns ovoid, scarcely 14×16 mm., rather loose in the cup, striately pubescent in the depressed end.

Ramuli juvenes ferrugineo-tomentulosi; folia elliptico-oblonga acuta basi cordata vix aliquanto undulata, 2-4×6-11 cm., infra flavicante-tomentulosa; petiolus tomentulosus, brevis; fructus annui, solitarii vel geminati, peduncule 4-5 cm. longo; glans ovoidea, basi, sublaxe inclusa.

The type is C. H. & M. T. Mueller no. 584—1933. The fruits were distributed with no. 597—1933 under the name *Q. consanguinea* Trel. & Muell. which may be regarded as a shade form of *Q. clivicola* having much larger leaves and called f. *consanguinea* Muell. f. nov.

A small or moderate tree with somewhat gnarled branches and deeply furrowed gray bark. Common on the drier openly wooded slopes.

Q. clivicola is apparently most closely related to *Q. glaucoides* Martens & Galeoti:

Leaves quickly glabrate, lightly glaucous beneath; petioles glabrescent; twigs soon glabrous.....	<i>Q. glaucoides</i> .
Leaves densely short hairy beneath; petioles and young twigs densely pubescent	<i>Q. clivicola</i> .

***Quercus clivicola* f. *crenifolia* Trel. & Muell. f. nov.**

Leaves more elongated-oblong, coarsely crenate, decidedly less pubescent beneath; petiole 7 or 8 mm. long. Pistillate catkins in summer about 50 or 60 mm. long, scurfy, several flowers at the end and about the middle sessile and singly disposed; the round cup with blunt scales, brown when glabrescent.

Folia elongato-oblonga; amenta fertiles 50 mm. longa, sursum pauciflora.

The type is C. H. & M. T. Mueller no. 585—1933.

***Quercus clivicola* f. *dentata* Trel. & Muell. f. nov.**

Scarcely differs from the species except that many leaves become acutely and coarsely mucronate-dentate upwards, the petioles rarely exceed 3 mm. in length, the single young fruit observed is borne on a peduncle only 3 mm. long.

Differt foliis inferioribus sursum acute dentatis; petiolus 3 mm. longus.

The type is C. H. & M. T. Mueller no. 583—1933. No. 584a is to be referred here also.

***Quercus microlepis* Trel. & Muell. sp. nov.**

(*Leucobalanus*—*Glaucoideae*)

Twigs slender (2 or 3 mm.), fluted, glabrous, gray-brown with numerous minute pale lenticels. Leaves deciduous?, hard-papery, oblong or occasionally subovate, obtuse, round-based or frequently somewhat cordate, entire or ex-

ceptionally shouldered near the end or mucronately toothed, $2-3 \times 5.5-7$ cm., bluish green, glabrous, flat or convallately cordate; veins about 10×2 , looping; petiole slightly downy, scarcely 5 mm. long. Catkins? Fruit annual, usually paired on a pubescent stalk scarcely 5 mm. long; cup saucer-shaped, 15 mm. in diameter, pale-tomentulose with contrasting small brown tips; acorn oblong, about 9×20 mm., covered near the base only.

Folia oblonga, apice et basi obtusa sive obscure cordulata, aliquando sursum subundulata, $2-3 \times 5-7$ cm.; petiolus 5 mm. longus; fructus annui, in pedunculo breve binati; glans oblonga, cupula subplana.

The type is C. H. & M. T. Mueller no. 578—1933.

A moderate tree with wide spreading branches and moderately fissured gray bark. Sparse on the openly wooded lower slopes.

Q. microlepis is most closely related to *Q. glaucoides* Martens & Galeoti (?) or *Q. baldoquinae* Trel. (?):

Cup scales somewhat thickened.

Petiole glabrescent, 5 mm. long. *Q. glaucoides*.

Petiole glabrous or stellate fleecy above, 3 mm. long. *Q. baldoquinae*.

Cup scales thin, appressed, petiole slightly downy, 5 mm. long. *Q. microlepis*.

***Quercus glaucophylla* v. Seemen var. *macropetiolata* Muell. var. nov.**

Rather densely branched, glabrous. Twigs slender (2 mm.), fluted, red-brown with minute pale lenticels. Buds round and blunt or ovoid and acute, some 2×2 or 3 mm., glabrate and brown, with setaceous stipules persistent above. Leaves deciduous?, blue-green and glabrous save for a few tufts of stellate hairs at the base of the midrib above, yellow granular, scantily stellate hairy and finely cobwebby with appressed simple hairs beneath, or entirely glabrate on both surfaces, chartaceous, obovate or subpandurate, undulately few-lobed upwards, obtuse at both ends, narrowly revolute, $2-3 \times 4-5$ cm.; veins about 8×2 , fine but prominent on both sides, very venose; petiole rosy, 5-10 or even 15 mm. long. Catkins? Young fruit sessile, globose, with appressed brown scales.

Glabrata; folia obovata vel subpandurata, utrinque obtusa sursum parcelobata, $2-3 \times 4-5$ cm.; petiolus 5-10 mm. longus, rubescens; fructus sessiles.

This variety differs from the type chiefly in its pubescence and the length of its petioles.

The type is C. H. & M. T. Mueller no. 574—1933.

***Quercus monterreyensis* Trel. & Muell. sp. nov.**

(*Leucobalanus*—*Aurantiaceae*)

Glabrate and very glossy. Twigs rather slender (2 or 3 mm.), fluted, gray with conspicuous pale lenticels. Buds subacutely ovoid, brown, glabrate, the terminal with persistent setaceous stipules. Leaves deciduous?, elliptic-sub-

obovate, subacute, obtuse or truncate-subcordate at base, entire or mostly coarsely crenate upwards, about 4×8 or 9 cm., gray- or olive-green above, yellow-olive and sparsely fleecy beneath; veins about 10×2 , scarcely looping; petiole 5–10 mm. long, orange. Pistillate catkins subsessile, with several flowers finally reduced to 1 or 2. Fruit annual, solitary or paired on gray-brown sparingly fleecy stalks about 10 mm. long; cup deep-saucer-shaped, 15 mm. in diameter with closely appressed gray-tomentose thickened scales, short fringed; acorn ovoid, scarcely half included.

Glabrata, nitidissima; folia elliptico-obovata, subacuta, basi obtusa sive truncato-subcordata, integra vel sursum obscure crenulata, $4 \times 8-9$ cm.; petiolus 5–10 mm. longus; fructus annui, solitarii vel geminati pedunculo breve griseo; glans ovoidea vix semi-inclusa.

The type is C. H. & M. T. Mueller no. 596—1933.

A moderately small tree with deeply furrowed, dark gray bark. Infrequent in the dense pine-oak-hickory forest of a high canyon.

Q. monterreyensis differs considerably from all other species in the section *Aurantiaceae*:

Petioles 3–6 mm. long; the contracted leaf base somewhat rounded. *Q. Standleyi*.
Petioles 5 to usually 10 mm. long.

Leaves rather acute at the contracted base. *Q. aurantiaca*.

Leaves subacute to usually subcordate at the base which is scarcely contracted
. *Q. monterreyensis*.

***Quercus Canbyi* f. *concolor* Trel. & Muell. f. nov.**

Scarcely differing from f. *adscendens* except in its distinctly narrower leaves, 3 or 3.5×6 or 7 cm.

A f. *adscendens* differt foliis angustioribus, $3-3.5 \times 6-7$ cm.

The type is C. H. & M. T. Mueller no. 590—1933.

***Quercus cupreata* Trel. & Muell. sp. nov.**

(*Erythrobalanus*—*Acutifoliae*).

Glabrous. Twigs slender (2 mm.), red-brown with minute pale lenticels, becoming gray with the lenticels more salient. Buds ellipsoid, acute, the scales ciliate and dark-margined, glossy, from reddish becoming clay-colored, 3×4 mm. Leaves narrowly lanceolate, aristately very acute, subcuneate, 3 or 4×10 or 12 cm., serrately lobed with long-setaceous points and U-shaped sinuses, dull blue-green and cancellate above, glossy copper-colored beneath; veins 8 or 10×2 , alternately passing into the points of the lobes; petiole pink, slender, 25 or 30 mm. long. Pistillate catkins in summer 5–15 mm. long with 3–4 flowers singly disposed. Fruit biennial.

Glabra; folia anguste-lanceolata, peracuta, aristata, subcuneata, $3-4 \times 10-12$ cm., serrato-lobata dentibus longesetaceis, infra cupreata; petiolus gracilis 25–30 mm. longus; amenta fertiles subelongata sursum sub 3-floris; fructus biennis.

The type is C. H. & M. T. Mueller no. 586—1933.

A moderate tree with graceful, spreading branches and deeply fissured, dark gray or black bark. Abundant in the dense oak wood on one high slope.

Q. cupreata apparently is most closely related to *Q. Grahmi* Benth:

Leaves setaceously serrate, typically rounded at base, buds ovoid, 2×3 mm.....
*Q. Grahmi*.
 Leaves lobed with long-setaceous points, typically subcuneate at base, buds ellipsoid,
 3×4 mm.....*Q. cupreata*.

***Quercus cupreata* f. *serrata* Trel. & Muell. f. nov.**

Differs from the species in the lance-elliptic, less bronzed leaves, aristately serrate instead of lobed, with petioles about 10–18 mm. long.

Differt foliis verdesscentibus lanceolata-ellipticis, minus profunde serratis, et petiolis brevioribus.

The type is C. H. & M. T. Mueller no. 595—1933.

***Quercus runcinatifolia* Trel. & Muell. sp. nov.**

(*Erythrobalanus*—*Acutifoliae*).

Glabrous except for rather evident leaf domatia. Twigs reddish with minute white dots becoming small but prominent lenticels. Buds ovoid, acute, 3×4 mm., grayish in age, glabrate. Leaves oblong, runcinately lobed with round sinuses and aristate points, acute at both ends, $5-7 \times 9-14$ cm., venulose on both sides; veins about 10×2 , like the midrib somewhat rosy beneath; petiole slender, tinged, 20–30 mm. long. Inflorescence and fruit?

Folia ablonga, aristato-runcinata, utrinque acuta, $5-7 \times 9-14$ cm., subtus domatiifera; petiolus gracilis, 20–30 mm. longus subrubescens.

The type is C. H. & M. T. Mueller no. 591—1933.

A moderate tree with spreading branches and deeply furrowed, dark gray or black bark. Abundant in the dense oak wood of one high slope.

Q. runcinatifolia is perhaps most closely related to *Q. Grahmi* Benth:

Leaves typically lanceolate, setaceously serrate with moderate sinuses...*Q. Grahmi*.
 Leaves various but with setaceous lobes and deep, rounded sinuses.

Leaves narrowly lanceolate and long attenuate, lobes entire, glabrous...*Q. cupreata*.

Leaves typically oblong or broadly lanceolate, lobes often toothed, dense tufts of axillary hairs beneath.....*Q. runcinatifolia*.

***Q. runcinatifolia* f. *lata* Trel. & Muell. f. nov.**

A broad-leaved juvenile form comparable with those of other species of the section, the domatia-bearing leaves 4×9 , 6×12 , or 8×15 cm., and undulately lobed with broad shallow sinuses and shorter awns than the species.

Forma juvenilis, foliis latioribus undulato-lobatis, 4-8×9-15 cm., breviter aristatis.

The type is C. H. & M. T. Mueller no. 593—1933.

Surrounded as they are on three sides by mountainous Northern Mexico, the Chisos Mountains of Western Texas would be expected to contain numerous outposts of Mexican vegetation. There appear several novelties; their abundance is partly explained by the close proximity of the little known Sierra Madre Oriental a part of the flora of which characterizes the Chisos Mountains.

Probably this situation accounts for the origin of the two species here proposed as a new section of the genus *Quercus*.

Erythrobalanus—**Robustae** C. H. Muell. sect. nov.

Small or large trees with stiff branchlets from stellate hairy to glabrate; coriaceous leaves aristately toothed and from densely tomentose to variously glabrescent, relatively long petioled; fruit biennial, the cups deeply cup-shaped with glabrate blunt scales.

Ramuli rigidi ex stellato-pubescentibus glabrati; folia coriacea aristatodentata, ex dense tomentosis varie glabrescentia; fructus biennis.

The stiff branchlets, leaves, and petioles as well as the greater pubescence and failure of the leaves to turn red in autumn distinguish the species of this section from those of the section *Coccineae* to which it is apparently most closely related. Autumnal coloration of leaves is a character not frequently used in the Southwest, perhaps because travel in the mountains is difficult late in the season and observations are consequently limited. The great brilliance of the foliage of *Quercus texana* var. *chisosensis* Sarg. changes entire mountain slopes from green to red. That the leaves of all the observed individuals of the section *Robustae* were deciduous without turning red or passed the winter in a green condition must be regarded as a character of considerable consequence. These habits were observed to be quite constant in the half dozen or more individuals of each of the two species which were examined during the autumns of two years.

Guercus robusta C. H. Muell. (*Torrea* 34: 119) the type. This species was reluctantly referred to the *Coccineae* at the time of its description, and its relation to *Q. texana* Buckley was cited.

Quercus tardifolia C. H. Muell. sp. nov.
(*Erythrobalanus*—*Robustae*).

A small erect tree with short, stiff branches. Twigs slender (2 mm.), somewhat fluted, at first densely tomentose with fascicled hairs, glabrous or nearly so in the second year and red-brown with minute inconspicuous lenticels,

becoming finally gray with the lenticels larger but none the more conspicuous. Buds acutely fusiform, $2 \times 3.5-4$ mm., hairy at the tip, the broadly truncate scales usually split at the end, slightly hoary and often ciliate. Leaves evergreen, the new ones appearing in dense tomentum about the first of July, moderate in size ($2.5-5.5 \times 5-9$ cm.), oblong-ovate to subobovate, 6 to 8-lobed by shallow or moderate sinuses, the lobes aristately tipped, entire or rarely 2-toothed, short and subright-angular like the apex, subequilaterally moderately cordate at the base, stiff coriaceous in texture, the upper surface dull blue-green, glabrate, the lower surface detachably stellate hairy; veins about 8×2 , alternately passing into the teeth, hardly evident above but prominent beneath; petioles rather stiff, $1-1.5 \times 15-20$ mm., red at the base, glabrate with the leaves. Catkins? Fruit biennial, young cups very similar to the same stage on *Q. robusta*, the scales thin appressed, short-truncate, hoary or glabrate possibly indicative of the elongated narrowly rounded mature scales of *Q. robusta*.

Ramuli ex dense tomentosis glabrati; gemmae acutae 3.5-4 mm. longae, 2 mm. crassae, squamis ciliatis; folia rigida oblongo-ovata vel subobovata, 5-9 cm. longa, 2.5-5.5 cm. lata, supra ex dense stellato-tomentosis opace glabrata, subtus laxe pubescentia, lobis 6-8 plerumque integris apice aristatis; petioli rigidi 15-20 mm. longi, 1-1.5 mm. crassi; fructus biennis, cupularum juvenilium squamis tenuibus adpressis breviter truncatis.

The type was collected by the author (without number) on July 3, 1932 in the Chisos Mountains of western Texas and is deposited in the herbarium of the University of Illinois at Urbana. Co-types may be seen at the New York Botanical Garden, in the herbarium of the University of Texas at Austin, and the author's herbarium at Cuero, Texas.

The species was encountered in only a limited locality in the oak wood above "Boot Spring" at an altitude of about 7,000 feet where it grows in a small clump much after the fashion of the straight trunks and stiff, horizontal branches of young trees of *Q. marilandica* Muench. farther east. It differs from *Q. robusta* in the late appearance of its evergreen leaves, its dense tomentum, and its erect shrubby habit as opposed to the large, widespreading branches of *Q. robusta*.

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Some diatoms of Great Salt Lake

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(WITH PLATE 6 AND ONE TEXT-FIGURE)

This study of the diatom flora of Great Salt Lake was made in connection with the investigations of Dr. A. J. Eardley, of the University of Michigan, on the geological conditions of Great Salt Lake. This lake, which is 4200 feet above sea level, is located in the northwestern part of Utah. Three fresh water rivers, the Jordan, the Weber, and the Bear rivers empty into it. The water, however, has a salt concentration approximately six times that of the sea. This concentration, due largely to the fact that the lake has no outlet, is so high that very few organisms can live in it.

A large body of fresh water, known as Lake Bonneville, occupied the bed of Great Salt Lake in Quaternary times. Its surface was more than a thousand feet above the present level of Great Salt Lake, and it covered a much larger area which was approximately equal to that of Lake Michigan. Due to evaporation and the closing of its drainage system, Lake Bonneville became more and more salt. Its salt concentration was for a long but indefinite period near that of the sea.

It was believed that the presence of diatoms in the various deposits might tell something of the past history of the lake. By means of a Musselman Peat Sampler, diatoms were taken from several depths. Surface samples were also collected.

The diatoms were cleaned by the acid method. Sometimes it was necessary to use soap solution in order to separate them from the clay. They were mounted in hyrax. A description of the samples taken and the various species found in each is given below. The symbols used for the various localities are those which Eardley employed in his paper. An appended map (after Eardley) shows the location of the stations from which various samples were taken.

Sample A. Blue-gray mud, under oolites. Collected at Rozell Point which is located on the northeastern shore of the lake.

<i>Cyclotella striata</i> (Kütz.) Grun.	Brackish water (marine, Boyer)
<i>Cymbella cymbiformis</i> (Kütz.) Breb.	Fresh water
<i>Denticula elegans</i> Kütz.	Fresh water
<i>Diploneis oculata</i> (Breb.) Cl.	Fresh water
<i>Diploneis</i> ? (a form intermediate between <i>D. puella</i> and <i>D. elliptica</i>)	
<i>Epithemia intermedia</i> Frische (acc. Pascher)	Fresh water
<i>Epithemia zebra</i> ? (Ehr.) Kütz.	Fresh and brackish water
<i>Fragilaria mutabilis</i> (W. Sm.) Grun.	Fresh water
<i>Melosira distans</i> (Ehr.) Kütz.	Fresh water
<i>Melosira granulata</i> (Ehr.) Ralfs	Fresh water

<i>Navicula bacillum</i> Ehr.	Fresh water
<i>Navicula bacillum</i> v. <i>lepida</i> (Greg.) Cl.	Fresh water
<i>Navicula cincta</i> (Ehr.) Kütz. acc. V.H.	Fresh and brackish water
<i>Navicula cryptocephala</i> Kütz.	Fresh water, rarely brackish
<i>Navicula peregrina</i> (Ehr.) Kütz.	Brackish water
<i>Navicula rhynchocephala</i> v. <i>amphiceros</i> (Kütz.) Cl.	Fresh and brackish water
<i>Nitzschia amphibia</i> Grun.	Fresh water
<i>Nitzschia apiculata</i> (Greg.) Grun.	Euryhaline
<i>Nitzschia epithemoides</i> Grun.	Brackish water
<i>Nitzschia subtilis</i> v. <i>paleacea</i> Grun.	Fresh and brackish water
<i>Pinnularia borealis</i> Ehr.	Fresh water
<i>Scoliopleura peisonis</i> Grun.	Brackish water
<i>Surirella striatula</i> Turpin	Euryhaline
<i>Synedra ulna</i> (Nitzsch.) Ehr.	Fresh water

Opephora—? This is an interesting form of which I found only a few specimens. Due to the shape and type of striae, I have placed it in this genus. Valve linear, clavate; length 31 microns, breadth 6–7 microns. Striae 8 in 10 microns. Plate 1, figs. 1, 2, 3.

There are many whole specimens as well as fragments of diatoms in this sample. The species characteristic of fresh to brackish water are most abundant as to numbers of individuals. There are, however, fresh water species represented. Also, there are forms which live in relatively high salt concentrations and are usually found in brackish to marine conditions.

These results support the geological findings that extensive swamps existed in this region in the very recent geologic past. These swamps, no doubt, had water of varying salt concentrations.

Sample Aa. Light gray mud, somewhat coarse, taken under fourteen feet of water, from the surface mud. Collected one mile east of Carrington Island, which is located in the southwest part of the lake. No diatoms.

Sample B. Blue-gray mud from Rozell Point, which is on the northeast shore of the lake, taken under two feet of water and twenty feet below surface muds by means of a Musselman peat sampler.

<i>Denticula tenuis</i> Kütz.	Fresh water
<i>Diploneis elliptica</i> (Kütz.) Cl.	Fresh water (also brackish-Boyer)
<i>Epithemia argus</i> v. <i>alpestris</i> (W. Sm.) Grun.	Euryhaline
<i>Fragilaria brevistriata</i> Grun.	Fresh water
<i>Fragilaria mutabilis</i> (W. Sm.) Grun.	Fresh water
<i>Melosira granulata</i> (Ehr.) Ralfs	Fresh water
<i>Navicula cincta</i> (Ehr.) Kütz. acc. V.H.	Fresh and brackish water
<i>Navicula radiosa</i> v. <i>tenella</i> (Breb.) V.H.	Fresh water
<i>Nitzschia hungarica</i> Grun.	Brackish water (also fresh-Boyer)
<i>Pinnularia Brebissoni</i> (Kütz.) Cl.	Fresh water
<i>Surirella striatula</i> Turpin	Euryhaline
<i>Surirella angusta</i> Kütz.	Fresh water
<i>Synedra affinis</i> v. <i>acuminata</i> Grun.	Fresh water
<i>Synedra affinis</i> v. <i>lancettula</i> Grun.	Fresh water

Many fragments of *Pinnularia* spp. and *Cymbella* spp. were found. The genera *Fragilaria* and *Denticula* were dominant. These findings indicate

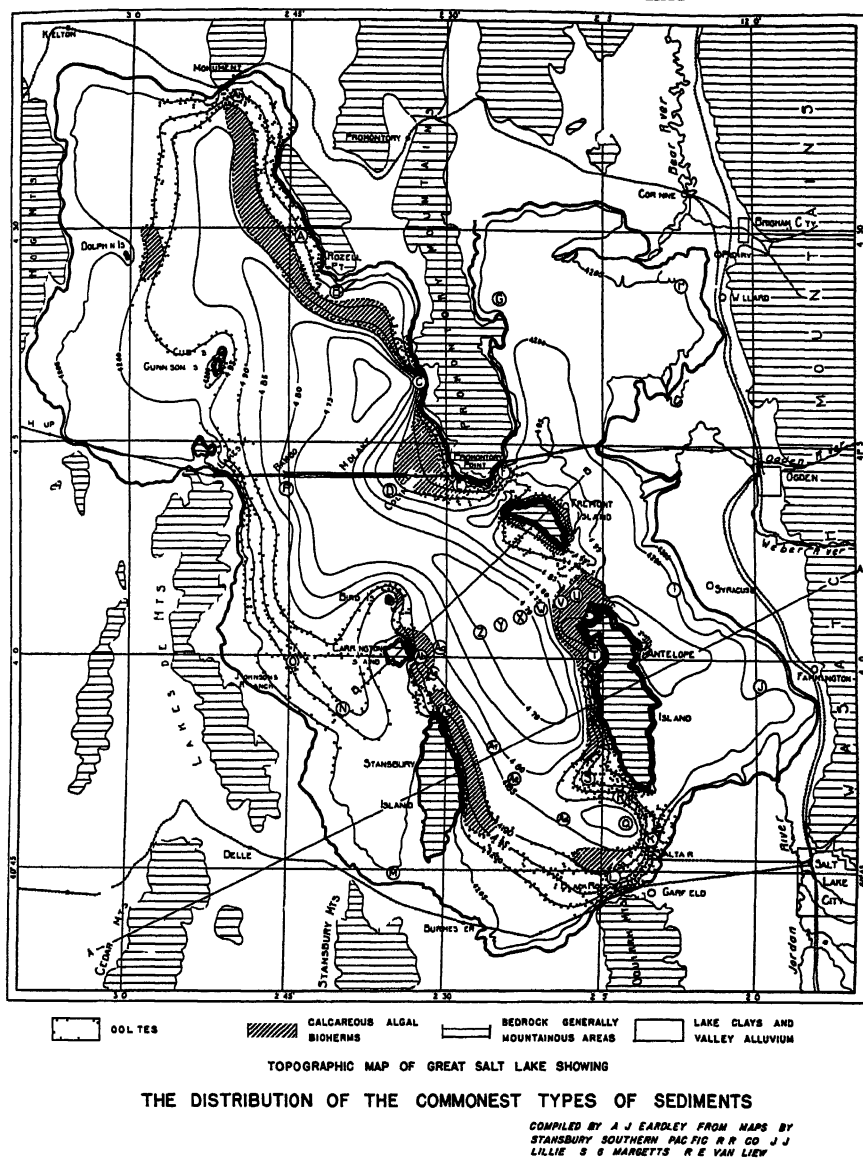


Fig. 1. Showing where the samples were obtained.

that the water at this depth was for the most part fresh. However, two euryhaline forms and three fresh to brackish water form were found. This might indicate a brackish tendency. According to the rate of deposit of

sediment in the lake, as determined by Eardley, these samples were about ten thousand years old.

Sample B₂. Fine, blue-gray mud taken from around oil seep craterlet at Rozell Point.

<i>Cyclotella comta</i> (Ehr.) Kütz.	Fresh water
<i>Epithemia sorex</i> Kütz.	Fresh and brackish water
<i>Eunotia gracilis</i> (Ehr.) Rabh.	Fresh water
<i>Fragilaria Harrisonii</i> (W. Sm.) Grun.	Fresh water
<i>Fragilaria mutabilis</i> (W. Sm.) Grun.	Fresh water
<i>Melosira distans</i> (Ehr.) Kütz.	Fresh water
<i>Melosira granulata</i> (Ehr.) Ralfs	Fresh water
<i>Melosira italica</i> (Ehr.) Kütz.	Fresh water
<i>Navicula cincta</i> ? Ehr.	Fresh and brackish water
<i>Pinnularia viridis</i> (Nitzsch.) Ehr.	Fresh water
<i>Stephanodiscus astrea</i> (Ehr.) Grun.	Euryhaline

Many specimens were found. Most of these species indicate fresh water conditions. Two fresh to brackish water forms and one euryhaline form were encountered. Evidently the mud was forced up from a much lower level.

Sample B₃. Green-gray craterlet mud from Rozell Point.

<i>Cocconeis placentula</i> Ehr.	Euryhaline
<i>Epithemia musculus</i> Kütz.	Brackish water
<i>Epithemia musculus</i> v. <i>constricta</i> (Bréb.) V.H.	Brackish water (Marine-De-Toni)
<i>Epithemia zebra</i> ? (Ehr.) Kütz.	Fresh and brackish water
<i>Navicula cincta</i> (Ehr.) Kütz. acc. V.H.	Fresh and brackish water
<i>Navicula cryptocephala</i> v. <i>pumilla</i> (Grun.) Cl.	Brackish water
<i>Navicula pygmaea</i> Kütz.	Fresh and brackish water
<i>Nitzschia amphibia</i> Grun.	Fresh water
<i>Nitzschia socialis</i> ? Greg.	Marine
<i>Rhopalodia gibberula</i> (Ehr.) O. Müll.	Euryhaline
<i>Scoliopleura peisonis</i> Grun.	Brackish water

Explanation of Plate 6

The photomicrographs and drawings are often of different specimens of the same species.

- Fig. 1. *Opephora*—? ($\times 1000$).
- Fig. 2. *Opephora*—? ($\times 1630$).
- Fig. 3. *Opephora*—? ($\times 1600$).
- Fig. 4. *Nitzschia* sp.? ($\times 1600$).
- Fig. 5. *Nitzschia* sp.? ($\times 1550$).
- Fig. 6. *Nitzschia* sp.? ($\times 1000$).
- Fig. 7. *Nitzschia*—? ($\times 1000$).
- Fig. 8. *Nitzschia*—? ($\times 1600$).
- Fig. 9. *Nitzschia*—? ($\times 1600$).



1



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4



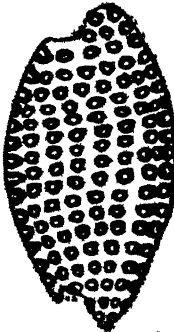
5



6



7



8



9

Nitzschia punctata ? (W. Sm.) Grun. The specimens which I found are closely allied to, if not the species *Nitzschia punctata* (W. Sm.) Grun. The main difference is in the number of striae. They are more numerous, averaging about 17 in 10 microns. Plate 6, figs. 4, 5, 6.

Nitzschia—? This is nearest to *Nitzschia granulata* Grun. However the double row of puncta in the keel are not evident. The valve is convex, elliptical with more or less acute ends. Length about 30 microns. Breadth is 15 microns. Striae are composed of large puncta, about six striae in 10 microns. Plate 6, figs. 7, 8, 9.

In this sample were many specimens of *Nitzschia*. However, the markings on the valves of many had been obliterated. Many specimens of *Epithemia musculus* Kütz., *Navicula cincta* Ehr., and *Scoliopleura peisonis* Grun. were found, which indicate more or less brackish water. As the water at this point is now very salt, it is evident that the mud was forced up from a lower depth. There is geologic evidence that fresh to brackish water swamps existed at this point in the past.

Sample D. Slightly coarse tan mud collected one half mile west of Colin in ten feet of water. No diatoms.

Sample F. Blue-gray and tan mud collected at Promontory Point, which is a southern point of Promontory Range. No diatoms.

Sample G. Tan clay, somewhat dried, no water cover at present, collected midway, east side of Promontory Range.

<i>Amphora proteus</i> Greg.	More or less euryhaline
<i>Caloneis amphisbaena</i> (Bory) Cl.	Fresh and brackish water
<i>Cocconeis scutellum</i> ? Ehr.	Brackish and marine water
<i>Cyclotella operculata</i> Kütz.	Fresh water (brackish-De-Toni)
<i>Cymbella aspera</i> (Ehr.) Cl.	Fresh water
<i>Denticula elegans</i> Kütz.	Fresh water
<i>Denticula thermalis</i> Kütz.	Warm water
<i>Epithemia sores</i> Kütz.	Fresh and brackish water
<i>Epithemia sores</i> v. <i>gracilis</i> Hust.	Euryhaline
<i>Epithemia turgida</i> (Ehr.) Kütz.	Fresh and brackish water
<i>Epithemia zebra</i> v. <i>saxonica</i> (Kütz.) Grun.	Fresh water
<i>Fragilaria mutabilis</i> (W. Sm.) Grun.	Fresh water
<i>Hantzschia amphioxys</i> (Ehr.) Grun.	Fresh and brackish water
<i>Navicula cincta</i> Ehr.	Fresh and brackish water
<i>Navicula radiosa</i> v. <i>tenella</i> (Breb.) V.H.	Fresh water
<i>Navicula viridula</i> v. <i>avenacea</i> (Breb.) Grun.	Fresh and brackish water
<i>Nitzschia hungarica</i> Grun.	Fresh and brackish water
<i>Nitzschia parvula</i> W. Sm. acc. Schönfeldt	Fresh and brackish water
<i>Pinnularia Brebissoni</i> (Kütz.) Cl.	Fresh water
<i>Pinnularia viridis</i> (Nitzsch.) Ehr.	Fresh water
<i>Rhopalodia gibba</i> (Ehr.) Müll.	Fresh and brackish water
<i>Surirella striatula</i> Turpin	Euryhaline

There is a mixture of fresh and brackish water forms. This mud has been the bed of some of the springs along the mountain base. There are numerous fresh water springs here, some of which are slightly sulphurous, while others are saline.

Sample H. Blue-gray and tan mud taken from fresh water canal, north-eastern part of lake. Collected west of Perry, near the dike to Bird Refuge.

<i>Amphora ovalis</i> (Bréb.) Kütz.	Fresh water
<i>Anomoeoneis polygramma</i> (Ehr.) Cl.	Brackish water
<i>Anomoeoneis sculpta</i> (Ehr.) Cl.	Fresh and brackish water
<i>Anomoeoneis sphaerophora</i> (Kütz.) Pfütz.	Fresh and brackish water
<i>Caloneis formosa</i> (Greg.) Cl.	Brackish and marine water
<i>Cymbella cistula</i> (Hemphr.) Grun.	Fresh water
<i>Diploneis oculata</i> (Bréb.) Cl.	Fresh water
<i>Diploneis ovalis</i> (Hilse) Cl.	Fresh and brackish water
<i>Epithemia turgida</i> v. <i>granulata</i> (Ehr.) Grun.	Fresh and brackish water
<i>Epithemia zebra</i> (Ehr.) Kütz.	Fresh and brackish water
<i>Gomphonema longiceps</i> v. <i>subclavata</i> Grun.	Fresh water
<i>Mastogloia Dansei</i> Thw.	Brackish or almost fresh water
<i>Navicula cincta</i> (Ehr.) Kütz. acc. V.H.	Fresh and brackish water
<i>Navicula cryptocephala</i> v. <i>pumila</i> (Grun.) Cl.	Brackish water
<i>Navicula oblonga</i> Kütz.	Fresh or slightly brackish water
<i>Navicula peregrina</i> (Ehr.) Kütz.	Brackish water (salt water-Hustedt)
<i>Navicula pupula</i> Kütz.	Fresh water
<i>Navicula salinarum</i> Grun.	Euryhaline
<i>Nitzschia apiculata</i> (Greg.) Grun.	Euryhaline
<i>Nitzschia punctata</i> (W. Sm.) Grun.	Euryhaline
<i>Nitzschia punctata</i> v. <i>elongata</i> ? Grun.	Probably euryhaline.
<i>Nitzschia sigmoidea</i> ? (Nitzsch.) W. Sm.	Fresh water
<i>Pinnularia viridis</i> (Nitzsch.) Ehr.	Fresh water
<i>Pleurosigma delicatulum</i> W. Sm.	Brackish and occasionally fresh,— De-Toni reports it from a marine locality
<i>Rhopalodia gibba</i> (Ehr.) Müll.	Fresh and brackish water
<i>Scoliopleura peisonis</i> Grun.	Brackish water
<i>Surirella ovata</i> Kütz.	Fresh water
<i>Surirella ovata</i> v. <i>utahensis</i> Grun.	Fresh and brackish water
<i>Surirella striatula</i> Turpin	Euryhaline
<i>Synedra acus</i> Kütz.	Fresh and brackish water

In this list we have a mixture of truly fresh water forms along with with fresh to brackish water species. Geological evidence points to the fact that this sample for the most part was laid down under brackish water conditions when the lake was at a much higher level. To the surface has been added the shells of fresh water diatoms now living in the fresh water canal. This, then, accounts for the curious mixture.

Sample I. Gray mud, no water cover, near eastern line of lake. Collected three miles west of Syracuse. The lake has recently withdrawn. No diatoms.

Sample J. Gray mud, somewhat dried, near the southeastern line of the lake. No water cover at present. Collected at Farmington about one foot below surface of mud. No diatoms.

Sample K. Blue-gray mud under oolites from southern part of lake. Collected at Salt Air. No diatoms.

Sample M. Tan mud from southwestern part of lake. Collected on lake bottom now dry, between Stanbury Island and the railroad track to south-east. No diatoms.

Sample O. Tan-gray mud, somewhat dried, no water cover at present from western side of lake. Taken eight inches below the surface at a point east of Johnson's Ranch and two miles inland from the present water line.

<i>Caloneis silicula</i> v. <i>minuta</i> (Grun.) Cl.	Fresh water
<i>Cyclotella Meneghiana</i> Kütz.	Fresh water
<i>Cymbella cistula</i> (Hemphr.) Grun.	Fresh water
<i>Epithemia argus</i> (Ehr.) Kütz.	Euryhaline
<i>Epithemia argus</i> v. <i>alpestris</i> (W. Sm.) Grun.	Euryhaline
<i>Epithemia zebra</i> (Ehr.) Kütz.	Fresh and brackish water
<i>Fragilaria mutabilis</i> (W. Sm.) Grun.	Fresh water
<i>Hantzschia elongata</i> ? (Hantzsch.) Grun.	Fresh water
<i>Melosira arenaria</i> Moore	Fresh water
<i>Melosira crenulata</i> (Ehr.) Kütz.	Fresh water
<i>Navicula gracilis</i> Ehr.	Fresh water
<i>Pinnularia Brebissoni</i> (Kütz.) Cl.	Fresh water
<i>Surirella striatula</i> Turpin	Euryhaline

There are many fragments as well as whole specimens in this sample. The predominant species are fresh water forms, although one fresh to brackish and several euryhaline species are found. This sample is hard to explain from the apparent geological history of the lake. The most probable explanation is that a thousand years ago there may have been numerous fresh water springs in this region, such as exist to-day on the east shore of Antelope Island, which run out on the lake bottom. Thus the existence of these fresh water forms may be explained.

Sample Q. Slightly coarse, tan-gray mud from the southern part of the lake. Collected four miles northwest of Salt Air in twenty feet of water. Only a very few broken fragments of diatoms were found. They were not large enough to identify as to species. These fragments were probably brought in by extraneous forces.

Sample T. Two samples were taken in White Rock Bay on the west side of Antelope Island, in the southeastern part of the lake. The samples were taken from the surface muds as well as three feet below the surface. No diatoms were found. The sediment is believed to have been deposited faster here than in other parts of the lake.

Sample Y. This sample was taken in the middle of the lake, southern part, one mile east of sample Z. No diatom flora was evident. A few frag-

ments of specimens belonging to the genera *Fragilaria*, *Melosira*, *Pinnularia*, and *Synedra* were found. They were so fragmentary that it is evident that they were brought in by extraneous forces.

Sample Z. Tan-gray mud was taken in the middle of the lake under twenty-five feet of water. It was taken east of Carrington Island. No diatom flora was evident. As in sample Y a few fragments were found which were evidently brought in by extraneous forces. Samples Y and Z were taken from the deepest part of the lake.

The results of these studies seem to indicate several interesting facts. The deepest samples taken, which were those by means of the peat borer, support the theory that a fresh water lake formerly occupied the region where Great Salt Lake now is. Ehrenberg (1870), and others noted the presence of fresh water deposits in Great Salt Lake. Eardley¹ states that the rate at which sediment is deposited is about six feet in ten thousand years. This rate varies in different parts of the lake.

The craterlet mud taken from the Rozell Point region is evidently clay which has been brought up from lower depths in the building of craterlets. The finding of these fresh and brackish water diatoms supports the geological theory of Eardley that swamps existed here in Pleistocene or early Post-pleistocene times.

Lake Bonneville, which was the fresh water lake that formerly occupied this region, gradually became more and more salt due to the lack of drainage and to evaporation. Therefore at one time it must have had much the same salt concentration as the sea, and this condition probably existed for a long but indefinite period. Moore (1899) has shown that the chemical composition of the water of Great Salt Lake is similar to that of the sea. Marine diatoms have been found to flourish in properly diluted water from the Great Salt Lake. In view of these facts it is interesting to note that truly marine forms seem never to have established themselves in the lake. Ehrenberg (1870) speaks of the rarity of marine forms. Of the few marine forms which he describes from this lake, that I have been able to trace, all, except *Coscinodiscus radiatus* Ehr., have since been found to be also brackish water forms. My studies also point to the fact that a marine diatom flora was never established in the lake.

No diatom flora is found living in the lake proper to-day. Daniels (1917) reports two diatoms from the denser waters of the lake. He states that they flourished when the concentration was reduced. He did not identify them as to species, and only approximately as to genera. My examination of the above mentioned surface muds, as well as of samples of living

¹ Eardley, A. J. Unpublished observations.

algae, which were taken from the lake proper, showed no evidence of a diatom flora. Living forms reported from this lake have been found, no doubt, in the surrounding brackish marshes and river deltas which have a much lower salt concentration.

The absence of living diatoms in the lake proper is to be expected in view of the fact that so few organisms can withstand the high salt concentration which exists in the present lake.

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INDEX TO AMERICAN BOTANICAL LITERATURE 1931-1935

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The response of plants to localized applications of various chemical agents

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(WITH PLATES 7-9)

In a preliminary report (Levine, 1934a), it was shown that small areas of plants, painted or injected with the carcinogenic agents of animals or with some of the products of the metabolism of the tumor producing organism, *Bacterium tumefaciens*, produced slight swellings and overgrowths. Gross sections through the treated areas showed an increased thickness of the wood together with a varying degree of meristematic hyperplasia. It was further shown that there was no difference in effects produced by single or repeated paintings, nor was there any difference in the effects produced by the different concentrations of materials used in these experiments.

The following report deals with the results of a further study on the effects of coal tar, scharlach R, dibenzanthracene and ammonium hydroxide on the sunflower, *Ricinus* and tomato. Also, further data are offered on the induced bending of given parts of the stems of plants after painting with coal tar and scharlach R. In addition, the effects of applying various organic compounds bearing the -SH group and those organic substances lacking in the sulfhydryl group on localized areas of various plants are reported.

The localized application of chemicals with the purpose of producing overgrowths on plants has received considerable attention. The literature has been frequently reviewed in connection with tumor formation on plants. Here it will suffice to call attention to those papers that deal more pertinently with the problems under consideration.

Magnus (1918) studied differences in reaction between the apical and basal portions of cross sections of the carrot root grown in Petri dishes. Magnus states that the apical surfaces produced callus tissue while the basal portion produced no growth. When both surfaces of the sections were treated with a culture of *B. tumefaciens*, both produced overgrowths with the larger reaction on the apical side of the section. The amount of callus formed was greater on the treated apical surface when contrasted with the nontreated sections.

Blumenthal and Meyer (1924) studied the effects of lactic acid on sections of carrot and stems of the geranium. The tissues were scratched and a 1% lactic acid solution was applied. While most of the carrot sections became molded, these authors contend that some produced overgrowths

[THE BULLETIN FOR MARCH (63: 115-176) WAS ISSUED MARCH 3, 1936]

which show morphological structures similar to those produced by the crown gall organism, *B. tumefaciens*.

Bittmann (1925b) studied the effects of weak solutions of lactic acid on a number of tap roots,¹ which he kept under cultural conditions. The paintings were made on alternate days. The resulting overgrowths he obtained, he attributed to the chemical stimulation of the lactic acid used.

Bittmann (1925a) also studied the effects of coal tar paintings on rabbit ears and came to the conclusion that the agent exerts its primary effects on the centrosomes. This rôle of the centrosome in malignancy in animals has recently been emphasized by Lewis and Lewis (1932). In the absence of centrosomes in the higher plants, it appears that crown gall and other reported overgrowths for these organisms cannot be referred to centrosomal behavior.

Auler (1925) investigated overgrowths on carrot sections, which he cultured in Petri dishes under aseptic conditions. He painted slices of these roots with 1/1000 of formic acid, formamid, and acetamid. Auler obtained small intumescences after 14 days, approximately the size and shape of peas, which were pale yellow in color. The formamid treated sections showed the greatest reactions, while those subjected to acetamid showed the least response. Histologically, Auler contends that the growth structure is not directly caused by the parasite, chemical or physical agent, but arises from the host tissue.

Rehwald (1927a) studied the effects of painting various concentrations of lactic acid more intensively than the former workers. He studied treated sections of roots,² leaves³ and radicles,⁴ and observed that repeated treatment with lactic acid tends to kill the new callus growths. I have been able to confirm these observations (Levine, 1934). Small nodules shrivel and disappear after continued painting with tar or scharlach R. Rehwald believes that the tumors formed arise from the cambium and on the bases of an histological examination of these tissues, he concluded that they are not unlike the overgrowths produced by inoculation with *B. tumefaciens*, as contended by Auler. In a later communication, Rehwald (1927b) reports further on the roots of the first mentioned series of plants and adds *Taraxacum officinale* and *Scorzonera hispanica*. He also added to his list of chemicals: 1% butter, propionacetic acid, formic acid and oleic acid copper. These were used in solution in ether or as a powder. The resulting overgrowths, Rehwald contends, are not due to the chemicals, for similar

¹ *Daucus Carota*, *Petroselinum*, *Apium graveolens*, *Brassica oleracea*.

² *Daucus Carota*, *Cochlearia*, *A Armoracia*, *Raphanus sativus*, *Brassica Napus* var. *esculenta*.

³ *B. sabauda*.

⁴ *Pisum sativum*, *Vicia Faba* and *Citrus Aurantium*.

growths were formed without treatments. Rehwald further stresses this conclusion in another brief report (1927c) in which he states that lactic acid or any of the agents used have no specific effect on the formation of new growths on the carrot or any other roots. Injury alone is sufficient for the development of similar overgrowths.

Kendall (1930) injected a series of organic compounds⁵ into growing stems of *Pisum sativum* and *Lupinus albus*. He reports that the reactions are characterized by a marked cytoplasmic enrichment of the parenchyma cells, renewed nuclear and cytoplasmic divisions which show irregularities such as polyploidy, and other aberrant chromosomal behavior. These reactions, Kendall states, were more pronounced after the treatment with acids and less marked after the injections with the enzymes. The controls, however, which were injected with distilled water, showed reactions very rarely.

Hammett, in 1928 and 1929, reported a series of studies on the rôle of organic compounds containing the -SH group on growth in animals and plants. Hammett pointed out that the roots of *Allium Cepa*, *Phaseolus vulgaris* and *Zea Mays* grown in water containing .05 mg of lead ($\text{Pb}(\text{NO}_3)_2$) for 24 hours take up the metal and deposit it in the growing center. The lead, Hammett believes, is combined in especially high concentrations with the nuclei and cell walls in this region. Cell proliferation is retarded, while cell elongation proceeds apparently unaffected. The dividing nucleus, Hammett and Justice (1929) contend, has a great avidity for lead and it is because of this that growth by cell proliferation is inhibited by the metallic ion. On the basis of microchemical tests of roots growing in solutions containing lead, Hammett believes that the lead is combined with an organic sulfhydryl compound analogous to and identical with glutathione.

Hammett contends that the root region of highest sulfhydryl concentration and mitotic activity contains a naturally occurring acid-stable, alkali-labile substance, a stimulator of root growth in length. Sulfhydryl is the essential stimulus to growth by increase in cell number. Cell size growth is not stimulated. Hammett and Reimann (1929) report that these theoretical considerations are supported by experimental data on animals. They applied thio-glucose to wounds made on the skin of normal rats. The treated skins, they contend, showed distinct acceleration of wound healing. On the basis of these observations Hammett interprets malignancy as the result of the stimulative effects of compounds bearing the -SH group. He believes that lines of cells, potentially tumor producing cells, sensitive to compounds bearing the sulfhydryl radicle, proliferate when an adequate concentration of this chemical is present.

⁵ Diastase, pepsin, saliva, formic acid, lactic acid and tartaric acid.

METHODS AND MATERIALS

The present report treats of the studies of the effects of coal tar, dibenzanthracene, scharlach R, ammonium hydroxide and other chemicals mentioned on the perennials: *Salix fragilis*, *Bryophyllum calycinum*, *Opuntia keyensis*, and *Carnegiea gigantea* started in 1933 together with the annuals: sunflower, castor bean, Jimson weed, Burley tobacco and tomato, grown in 1933-4-5. These plants were all grown in a well lighted and manured open garden on the Montefiore Hospital grounds. Localized areas of the stems of thirty willow trees, 7 to 12 feet tall were painted with either 0.5%, 2% or 4% coal tar in ether or $\frac{1}{2}$ % or 1% scharlach R in ether three times a week. The paintings were started on August 3, 1933 and continued to December 25, 1933. The paintings were resumed on July 16, 1934 and continued to November 11, 1934. During the current year the plants were not treated but were carefully studied as to growth in general and in particular the reactions of the painted areas of the stems. The paintings of the cactus and the *Bryophyllum* plants were made with the same suspensions, started in June 3, 1933 and were continued weekly to April 13, 1934. These plants were grown in large pots in the greenhouse and were removed to the garden during the spring and summer months. The paintings were resumed on July 18, 1934 and continued to October 25, 1934.

The annuals reported before (Levine, 1934a) were studied during the growing season in the garden. They were treated with coal tar or scharlach R suspended in ether. The dibenzanthracene was applied in olive oil. In addition, a large number of each of the following plants: sunflower, *Ricinus*, *Datura*, *Nicotiana glutinosa*, *N. tabacum*, and tomato were injected with one of the following substances: .25% parathiocresol in ether, 1% thiophenol, 1% thioglycollic acid, and 1% tryptophane, each dissolved in distilled water. Weak solutions of hydrogen sulphide and ammonium hydroxide were also used. Pure, carefully prepared glutathione, cysteine, 1-cystine, glutamic acid or glycine was used in powder form.

These solutions were introduced into the lumina of such plants as the *Datura* and *Ricinus*, while cavities were formed in plants with solid stems, by introducing large bore syringe needles which removed cylinders of tissue corresponding to the lumen of the needle. The powdered substances were introduced into small injuries made by ten to fifteen pricks of a sterile steel needle. Numerous controls were made by injuring only the actively growing portion of the stem. *B. tumefaciens* was introduced into a number of plants of each species. This served as a possible index of the tumor producing power of the plants used under the conditions under which the treated plants were growing. More than 600 annuals were used in 1934 in these experiments. More than 300 of the same species of annuals were

grown in 1935 to check certain phases of the results obtained in 1933 and 1934.

Young branches of three 15-year-old apple trees were amputated and the cut surfaces of the branches were painted weekly beginning July 27, 1934 to October 11, 1934 with a 1% solution of coal tar in ether or a similar solution of scharlach R in ether. These branches were carefully labelled and the callus formations were carefully noted.

The plants were fixed at supposedly critical stages in the development of the reaction tissues. These fixations were abundant and at relatively short intervals. Coal tar treated plants were fixed after each painting from the first to the twentieth. Plants fixed after prolonged treatment were found to be too woody to section for microscopic examination.

The tissues were fixed principally in Bouin solution and Flemming weaker fixative. The material was imbedded in 52°-54° paraffin and sections were made 5 μ , 7.5 μ and 10 μ thick. Flemming's triple stain was used. Light green dissolved in oil of cloves was used after staining with an aqueous safranin. This was found to be a very desirable combination of stains for morphological studies. The nuclei take on a ruby red color with the safranin while the cytoplasm and cell walls take the light green in different intensities.

OBSERVATIONS

In a preliminary report (Levine, 1934a) on the effects of treating plants with the carcinogenic agents of animals, it was pointed out that the young injured portions of the sunflower stem painted with coal tar or scharlach R suspended in ether or pentane, in concentrations varying from $\frac{1}{2}$ % to 10%, produced swellings in the area of treatment. The swellings, in gross longitudinal or cross section showed increased thickness of the wood together with increased parenchymatous tissue. Stems of the *Ricinus*, when similarly treated, showed an overgrowth of tissue in the lumen of the stem. There was no macroscopic evidence of superficial overgrowths such as were described by Auler, Blumenthal and Meyer, Bittmann, Kendall and others, on taproots after painting with lactic or formic acids. There was macroscopic evidence that proliferation of tissue had occurred in excess of the numerous controls which were injured or treated with ether only. The plants inoculated with a virulent strain of *B. tumefaciens* showed the characteristic surface overgrowths now well known.

It was pointed out in that report that painting one side of the growing point of sunflower plants with ether and coal tar or scharlach R inhibited apical growth and induced open S-shaped curvatures of the stem in a large number of plants treated.

Treatment of the apical portion of sunflower stems

During the growing seasons of 1933, 1934 and 1935 more than 200 actively growing sunflower stems were treated with ether or pentane suspensions of coal tar or scharlach R. Four sets of experiments were made each year. Some plants were injured and painted at the growing region of the stem; some were just painted without injury; stems of some plants were injured and painted at the fifth and sixth leaves and some were just painted in that region. In the majority of the plants in which the growing region was painted either with scharlach R or coal tar in ether or pentane, injured or non-injured, there was a bending of the stem.

Figure 1 (pl. 7) represents two sunflower stems treated with ether and coal tar. The paintings began on June 10, 1933 and were continued to August 7, 1933. The longitudinal section in figure 1A shows the callus formed about the injured areas in the pith. The growing point has been disturbed so that there are two or three shoots arising from an arrested thickened stem. Figures 4 and 5 (pl. 7) represent longitudinal sections of two stems, one showing the cut surface. The plants were painted weekly with a 10% solution of ether and coal tar. In all, four paintings were made. The gross effects are the same as those of the injured stems. The growing region, as in the case of the injured stems, breaks up into a number of growing centers and two or more attenuated short stems are formed. There appears to be no thickening of the tissue, although it seems as if the stem at the painted areas showed a reduction in the thickness of the stem. It has already been pointed out that scharlach R suspended in ether produces similar effects.

Under certain conditions the stems bend slightly but recover and appear almost straight as in the normal. In figure 2 (pl. 7) two plants are shown, one treated with ether and coal tar (A) after injury at the growing region, the other treated with scharlach R in ether (B) below the growing region. The latter seems to have been but slightly affected. There is considerable swelling above the painted area but little bending. The coal-tar ether treated stem is dwarfed with the interfoliar spaces greatly reduced. The axillary buds develop into shoots which bear heads, producing a witches' broom effect. Pentane used as a solvent does not alter the reaction of the plant to the coal tar or scharlach R. Figure 3 represents photographs of two plants: "A" was injured and given four weekly paintings with ether. There appears to be a shortening of the interfoliar spaces, but with no bending of the stem. The photograph shown in figure 3B represents a plant that was injured and treated with coal tar dissolved in pentane. This plant was treated below the growing point over a large area

and appears to have involved the active region of the growing stem. Recovery from bending appears to have started.

During the current year these experiments were repeated and it appears that unilateral painting of the growing region of the sunflower stem induces bending. The stem is dwarfed and frequently a number of growing centers are activated, which produce stems that bear flower buds. When the treatment is applied to the stem below the growing region, there is little bending, from which the stem recovers rapidly. The injured area shows considerable swelling.

The mechanism involved in the bending of the treated stems is not clear. There appear to be a number of possibilities that may explain these phenomena. It is possible that as few as four paintings with the irritants are sufficient to inhibit the growth and division of the cells. This may be due to some osmotic change in the superficial cells as shown by Ortiz Picón (1932) and Levine and Bergmann (1936). The coat of tar or scharlach R may prevent the escape of catabolic substances while the anabolic products of the cells may stimulate unpainted normal areas. This fact is not entirely clear on the basis of sectioned material reported below. It is suggested, on the basis of the work of Went (1928) and others, that the growth hormone or auxin in the growing region of the stem is affected by the coal tar, scharlach R and probably a variety of substances still unknown, so as to interfere with the normal growth and division of the cells. The development of swellings which occurs at the injured area of the stem after painting with coal tar and scharlach R and the other chemicals referred to below seems to affect the deeper layer of cells, especially the cambium, which proliferates. This implies the movement of the growth hormone from the injured cells to the surrounding tissue. Studies on the growth hormone in the stems of the sunflower and other plants, to verify, if possible, these concepts of the mechanism of tumor formation in plants, is now in progress.

Further, it has been stressed by a number of workers that the mechanism of tumor formation in plants after inoculation with *B. tumefaciens* is not due directly to the presence of the organism itself. It is suggested here that the organism may stimulate the host cells by the liberation of growth stimulating substances. These cells are capable of perpetuating themselves for a limited number of generations while the supply of these substances lasts. It has been shown (Levine, 1936) that the *B. tumefaciens* organism when grown under cultural conditions undergoes morphological changes. These changes may be associated with physiological alteration in the parasite. Old cultures of *B. tumefaciens* are not as virulent and do not produce crown galls as readily as young cultures of the organism.

The effects of the -SH group

To study the effects of the chemicals containing the sulfhydryl group upon young plants, *Helianthus annuus*, *Ricinus communis*, *Datura stramonium* and *Nicotiana tabacum* were injected with or injured areas were powdered with glutathione, cysteine hydrochlorate, 1-cystine, parathio-cresol, thioglycollic acid or thiophenol. To better study the effects produced by these chemicals, some organic compounds without the sulfhydryl group were used, namely: glycine, glutamic acid and tryptophane. Coal tar in ether and dibenzanthracene in olive oil paintings were also made on a smaller number of plants, and ammonium hydroxide and hydrogen sulphide in weak dilutions were injected into another group of plants of the same species. The control plants were merely injured or inoculated in the usual manner with *B. tumefaciens*.

Glycine, glutamic acid, 1-cystine, cysteine, glutathione and dibenzanthracene were applied to growing portions of young sunflower plants four to five feet tall. These substances were chemically pure and they were applied by means of a sterile wooden probe sharpened to a point, which was used to injure the plant and at the same time to introduce the agents into the tissues. Each plant was carefully labelled after the treatment. The plants were observed daily and it was noted 24 hours after treatment that slight necrosis appeared about the injuries. One week after the sunflowers were treated, it was noticed that the glutathione treated stems showed greater reactions in the form of swellings and small intumescences. Two weeks after the treatment, the glutathione treated plants showed the largest reactions of any of the treated plants and equal to the swellings produced by *B. tumefaciens*. The maximum reactions shown by the control plants were slight or moderate swellings.

The treated sunflowers were removed from the garden and sorted and measured. Longitudinal sections were made of most stems. It was noticed that the growths produced by glutathione, glutamic acid and dibenzanthracene were not much different. The *B. tumefaciens* inoculations were not as large as they had been in previous years. The comparison was made on the basis of photographs previously made.

Figures 1 to 12 (pl. 8) show a series of photographs of the sunflower stems and their longitudinal sections thirty to forty days after treatment with the various chemicals. Figures 13 and 14 represent control sunflower stems. The former shows considerable swelling in longitudinal section. Figure 2 represents a stem of the sunflower treated with glutamic acid after injury. The small intumescences are of interest and it appears as though a tumor mass is imbedded within the host tissue. Gross section (fig. 1, pl. 8) shows new wood formation and considerable parenchymatous

tissue. Microscopic examination of these stems is referred to below. It may be said, however, that the microscopic sections show considerable hyperplasia. The reactions of the sunflower stem to parathiocresol (figs. 7 and 8) are very characteristic and differ from the reactions of other plants in that thick irregular masses of tissue resembling distorted calluses are formed. The formation of wood after treatment with parathiocresol is very extensive and microtome sectioning of this tissue without the use of special methods is extremely difficult.

Growing internodes of *Ricinus* plants were injured and treated with glutathione, glycine or cysteine hydrochlorate. After three months these stems were removed and studied. The surfaces where the injuries were made were closed by scars. Longitudinal sections of these stems showed the lumina of the injured internodes filled with parenchymatous tissue in which vascular elements were found. There was no difference between the reaction of the *Ricinus* to the -SH group bearing chemicals and those that had no sulphhydryl elements in it. Figures 18, 19, 20 show the reaction of *Ricinus* to suspensions of dibenzanthracene in olive oil. While the quantity of dibenzanthracene differed, the reactions were approximately the same. Figure 18 shows a surface view of a small stem treated with .001% dibenzanthracene in olive oil. The stems shown in figures 19 and 20 received .01% dibenzanthracene. Longitudinal sections show the same type of reaction in the lumina of the stems as produced by the glutathione. I have made too few controls on the *Ricinus* but from evidence already present it appears that any internal injury to the parenchyma of these stems sets up a reaction which results in the overgrowth of the parenchyma. This new growth which fills the lumen of the injured and treated internode with the tissue, shows fibrovascular elements. This type of tissue represents the most effective reparative protection tissue the plant seems to be capable of producing.

B. tumefaciens inoculations in the *Ricinus* results in the formation of localized masses of tissue about the point of inoculation in the lumen of the stem and on the surface. Frequently the new growth fills the lumen of the internode inoculated. *Ricinus* stems were injected with 1% thiophenol and 1% thioglycolic acid. A 1% tryptophane suspension was also used. Approximately 1 cc. of the solution was injected into a young internode. It was observed that the treatment produced wilting of the stem at the injected internode. The internodal tissue became soft and collapsed due to the weight of the tissue above it. There was recovery, however; the tissue became turgid but never recovered its normal shape or position. In a number of cases the apical portion of the injected stem died, while a smaller number survived.

Few plants showed evidences of parenchymatous reaction in the lumina of the stems after treatment with the thioglycollic acid. Where there was a splitting of the tissue in the survived stems, considerable callus was formed. There was no evidence of overgrowths comparable to crown gall formation.

Ricinus stems treated with tryptophane showed scar tissue but no internal reactions. Thiophenol produces no marked reaction of the tissue in the *Ricinus* stem. Hydrogen sulphide solution in small quantities was also injected into the lumina of a number of stems. There was slight callus formation at the point of injection but no further reaction.

Stems of *Ricinus* and *Datura* plants were injected with 1% solutions of ammonium hydroxide. These injections were started in July, 1934 and were continued weekly to October of the same year. The *Ricinus* plants were injected in one of the upper internodes with 5 cc. of the solution, while the *Datura* stems were injected with 20 cc. The stems of the *Datura* plants are not septate so that the fluid accumulated in the hollow of the central stem. The stems of the *Datura* were cut longitudinally from the branch injected to the root of the main stem. A large quantity of the solution had accumulated at the base of the stem. It is reasonable to assume (Smith, 1917) that small quantities of ammonia gas were liberated in the lumen of the stem. In both species of plants scars formed about the points of injection but no hyperplasia of the tissues was found.

The *Ricinus* stems wilted at the internodes injected, resulting in death of the apical portion of the stem. A comparatively large number recovered, leaving the stem twisted at that node, an effect produced by the solutions referred to above. The lumen of the plant showed no proliferation of parenchyma. It appears as though the solution destroyed the living parenchyma which proliferates abundantly after treatment with most of the other chemicals used. Stems of *Datura* treated with glutathione, cysteine, glycine and glutamic acid produced scars, but in no case was overgrowth tissue found. Scharlach R and coal tar treated stems of Jimson weeds showed abundant surface intumescences as shown in figures 23 and 24 (pl. 8) respectively.

Continued paintings of *Ricinus*, willows and apple with coal tar show thickened calluses about the painted injured areas. Figure 21 (pl. 8) shows the effects of treating young *Ricinus* stems with coal tar in pentane for more than four months. The plants became old, flowered and produced abundance of seeds. The painted internode shows a warty mass of corky tissue. The control (fig. 22) treated with ether after injury for the same period of time shows a small internodal space but no further reaction. The lumina in both cases were filled with woody tissue characteristic of the basal internodes of the plant.

Young willow trees raised from cuttings were painted with coal tar or scharlach R weekly and thrice weekly for a period of ten months in 1933 and 1934. The calluses about the injured areas were removed four times at intervals of about two months. No overgrowths other than heavy calluses were formed. The wood which was exposed several times was completely covered. It appears that the tar treated plants healed faster and may indicate the use of coal tar as an effective agent in horticultural practice.

The midvein of the Burley variety of *N. tabacum* was injured and then subjected to powdered glycine, glutamic acid, glutathione, cysteine hydrochlorate and dibenzanthracene in olive oil. Fifty such plants were used with one to three leaves on each plant treated. Two days after treatment with cysteine, necrosis of the area treated resulted in loss of the leaf. The glutamic acid and glutathione produced necrosis to a moderate degree. The surviving leaves were harvested and examined three months after treatment. In no case was there any gross evidence of embryonic proliferation or tumor formation. Scars were formed and the treated areas healed.

The growing tips of thirty tomato plants were subjected to 1% thioglycollic acid, 1% parathiocresol, dibenzanthracene and glutathione. The glutathione treated stems showed thick scars with occasional splitting of the tissue and healing about the injuries. Puckering of the tissue about the wound appears greatest in the dibenzanthracene treated plants, three months after treatment, as shown in figure 16 (pl. 8). The injured controls show slight or no reaction except a series of concentrated needle pricks. Tomato plants growing in the same plot, inoculated with *B. tumefaciens* produced the typical crown gall as shown in figure 17 (pl. 8). The parathiocresol, thiophenol and thioglycollic acid produced necrotic areas with little or no reaction tissue.

In Jimson weeds subjected to the same treatment as the tomato, the reactions were more favorable. Thick scars were formed at the point of injection with thioglycollic acid and parathiocresol. The lumen of the stem showed proliferation of parenchymatous tissue especially about the site of injection.

The *Bryophyllum* and cactus plants reported previously showed no further reaction. No joints or proliferating branches were found in the painted portion of the plant. The actively growing stem showed larger calluses than smaller plants. The callus seemed to be thicker and formed more rapidly than those of the controls. Injected notches of *Bryophyllum* leaves that usually form crown galls after inoculation with *B. tumefaciens*, produced very slight reactions. Of the large number of leaves treated many of them were shed forty-eight hours after treatment.

Seedlings of sunflower and *Ricinus* were studied in pots in the laboratory and in the garden. The potted plants were painted with coal tar or

scharlach R. More than 118 sunflower plants with first leaves were treated with the entire range of chemicals used on the more mature plants. The potted plants reacted poorly to the treatments. Even the inoculation with a virulent strain of *B. tumefaciens* resulted in minute papillae at each point of inoculation. There were evidences of small swellings about the injuries, which consisted of a single prick of a pointed probe.

The sunflower seedlings grown in the garden grew rapidly and responded like the old plants. Sections through these seedlings 45 days after treatment with the sulfhydryl bearing chemicals showed corky swellings. The greatest reactions were obtained with parathiocresol.

In general, it may be concluded that the various chemicals showed little difference in their effects upon the plants used. Plants treated with glutathione, glutamic acid and dibenzanthracene appeared to show the greatest reactions. The compounds not bearing the -SH group showed marked reactions dependent upon the health and vigor of the plant used. This, it appears, is no argument against the importance of the -SH group in growth, but it rather points to our inadequate knowledge concerning the plants and stimuli. How coal tar, dibenzanthracene and the other carcinogenic agents produce cancer in animals is still unknown. It is clear, however, that a large number of chemicals exert a growth stimulating effect on plant cells locally treated. At present it appears that the intervention of another living organism such as the fungi or the nematodes is required to produce overgrowths in the higher plants.

The histology of chemically treated stems

An abundance of material from the different species of plants treated with various agents mentioned above, was prepared for microscopic examination. A large number of microscopic preparations were photographed at low magnification for the purpose of comparing them with the control tissues consisting of injured stems and crown galls. In plate 9 a small number of these photographs is shown. As I have pointed out in 1934, none of the chemicals used produces overgrowths comparable in size to those produced by *B. tumefaciens*. The histology of these overgrowths at comparable ages is different.

In young crown gall tissues the elements consist of disoriented parenchyma, protoxylem, and xylem elements. In the chemically treated tissues the same types of cells appear, but the disorientation and the bizarre effects appear to be less striking. While the cellular elements are necessarily the same, crown gall tissue differs from the chemically induced reaction growths in that the peripheral cells are nucleated and actively proliferating; growth is peripheral. In the chemically induced reactions

the peripheral cells, those nearest the seat of injury frequently hypertrophied, are large and mature and generally show no nuclei. Nuclear and cell divisions occur in cells surrounding the peripheral layer of cells. Parenchymatous tissue with fibrovascular elements occur in both types of tissue. However, there are variations of this state, as mentioned below. Cytological studies of tissues twenty to thirty days after treatment show large cells with small nuclei. These appear to be mature cells at this time and do not present embryonic appearances characteristic of neoplastic tissue. Few division stages have been observed. In preparations made a week after treatment, proliferating cells have been observed. The cell and nuclear divisions are normal and the chromosome groups are relatively clear. There is no evidence of polyploidy in these preparations although no special study of chromosomes has been made. Binucleate cells are of frequent occurrence.

It has been pointed out above that crown gall tissue presents certain characteristics that differentiate it from the chemical reaction tissue. Figure 4 (pl. 9) represents a photomicrograph of a section of a crown gall on the sunflower 49 days after the stem tissue was inoculated with *B. tumefaciens*. The active cells occupy a broad peripheral margin of the gall. The cells are small, embryonic in appearance, and are typical of crown gall tissue (Levine, 1931). The terminal cells have formed a corky covering over the surface of the gall. Hypertrophied, large, parenchymatous cells also form part of this tissue.

Scar tissue formed after injury, in a control plant, is shown in figure 1 (pl. 9). This specimen was taken from a sunflower stem five weeks after needle wounds were made in the young terminal portion of the stem. The surface of the section shows corky cells. The tissue lying on both sides of the deeply stained area of injury, shows layers of hypertrophied cells; few nuclei are present. There is evidence that in the development of the new tissue, the cells were active, but at this period the cells are mature or old. A tendency to form a corky covering over the injured area is obvious.

Sections made of control sunflower stems, 5, 21 and 27 days after injury show in the first case, considerable proliferation of the meristematic tissue around the fibrovascular bundles. The cells are small with comparatively large nuclei. The cells about the injury appear hypertrophied. The stimulation of the meristematic cells in the control specimens results in extensive proliferation of this tissue; the cells mature early and form considerable wood which increases the thickness of the stem above the normal. This is evident in specimens 27 days after injury. Space will not permit the publication of these photographs. Histologically, these preparations resemble closely the chemically treated stems.

Coal tar suspended in ether when applied to injuries in stems of the tobacco (*N. tabacum*) produces small scars about the surface injury and woody tissue is formed about the traumatized tissue in the pith. The thickness of the wood is increased as shown in figure 15 (pl. 8). Fixation of the scar tissue has in several cases revealed the presence of internally formed embryonic rootlike structures as shown in figure 2 (pl. 9). The embryonic reaction tissue is present but surrounded by a mass of parenchymatous cells; one observes small thick-walled cells from which the embryonic rootlike structures make their appearance. These bodies resemble the rootlike structures observed in crown gall on *Opuntia keyensis* (Levine, 1934 b). The presence of these embryonic rootlike structures does not imply that coal tar is specific for these *Anlagen*. The cellular reactions in the tobacco are abundant and capable of differentiating into these embryonic growths. No embryonic leaves were observed. The evidence from the present studies and those on crown gall previously reported, seems to indicate that the tobacco is capable of responding in this manner. One may conclude that the type of response is a function of the host rather than the stimulus.

The selected area shown in figure 2 represents only one of many of these regions in the treated stem, in which the embryonic structures could be definitely identified as the longitudinal sections of roots. Some of the structures were further advanced than the one shown in this figure. Sunflower stems treated with coal tar for five weeks during which time nineteen paintings were applied to a small injured area of the stem, showed considerable swelling. On sectioning the stem through the injured area one finds a mass of necrotized cells. Radiating from it are slightly hypertrophied cells with smaller embryonic types of cells on the surface of the mass of tissue, surrounding the area of injury. The whole is buried between strands of fibrovascular bundles. Meristematic tissue is involved in deep injuries. Protoxylem cells are found and the xylem appears later. These injuries present distinct pathological structures which are not readily separable from the crown gall tissue. The extent of the reaction varies in the different species and in the individuals in a species. These sections differ little from those of stems treated with dibenzanthracene.

Specimens of sunflower stems painted once with coal tar in ether and fixed twenty-two days after the treatment showed a prolonged duration of the proliferation period, thus forming a great mass of embryonic cells. This suggests the possibility that the repeated paintings induce early maturity of the treated tissues, due possibly to interference with the metabolism of the newly formed cells.

Figure 3 (pl. 9) represents a section of a sunflower stem treated with coal tar in ether once weekly for ten weeks. The reaction tissue is clearly

shown in the upper part of the photograph, while the normal cortical tissue is seen in the lower part. Note the binucleate cells in this tissue. Histologically this tissue is quite comparable to crown gall (see fig. 4, pl. 9). The principal difference between these tissues appears to be one of quantity. In both reactions, crown gall and chemical stimulation, there are cellular proliferations at first and then differentiation; the types of cells involved are the same. The chemically stimulated tissue has a short embryonic life, while crown gall proceeds further in piling up a greater mass of embryonic tissue before differentiation and old age set in. In animal and human cancer, cell proliferation is generally considered limitless. While the animal and human pathologist can, in most cases, recognize malignancy and overgrowths on the basis of a microscopical examination of the tissue, in plants the absence of an overgrowth makes the diagnosis of a tumor, such as crown gall, difficult.

Sunflower stems treated after injury with compounds bearing the sulfhydryl group show microscopically a layer of large cells about the traumatized tissue, surrounded by a layer of small, active, embryonic cells. In this, the reaction is identical with the nonsulfhydryl bearing compounds used in these experiments. Figure 5 (pl. 9) represents a section of a sunflower stem ten days after injury and a single application of tryptophane. This section was made through the reaction tissue. The upper surface of the figure represents the traumatized cells, while the active cells occupy the central portion.

Stems treated with thiophenol, parathiocresol, cystine, cysteine, glutamic acid and glycine give similar reactions. Preparations of sunflower stems made after treatments with these chemicals are so much alike that one cannot be separated from the other.

In glutathione preparations such as the one shown in figure 6 (pl. 9), the overgrowth consists of stimulated meristematic tissue coupled with hypertrophy. The upper margin of the figure represents the injured cells. Below this layer, as in all the chemically treated tissues, one finds the mature parenchymatous cells and below this, the layer of active cells. In this specimen, the active cells appeared larger than usual.

According to Eckert, Cooper and Seelig (1935), scharlach R is not carcinogenic for young white rats. In these plant studies, the scharlach R treated sunflowers very frequently elicited greater swellings than any of the chemicals used.

Figure 7 (pl. 9) represents a section of a tomato stem painted four times from the 12th of July to the 19th, with scharlach R suspended in ether. The necrotized tissue runs through the middle of the figure. Hypertrophied and hyperplastic cells are seen on both sides of this area.

Binucleate cells are common, although the chromosome number was not definitely established. The chromosome masses in these cells appeared of uniform size. Here again, as in figure 3, we have all the characteristics of young, undifferentiated crown gall tissue lacking, however, in the proliferating power and quantity of tissue to form an overgrowth. None of the chemically treated stems produced overgrowths comparable with the crown gall or other neoplastic tissues in plants.

SUMMARY AND CONCLUSIONS

1. A further study of the effects of treating plants with various chemical substances is reported.

2. Painting the apical part of the stem of the sunflower each week with a solution of coal tar in ether or pentane or scharlach R in ether, produces bending of the stem. The plant remains dwarfed and the growing point often gives rise to several small apical branches, producing a witches' broom effect.

3. Stems of sunflower, *Ricinus*, *Datura*, tomato, tobacco and leaves of tobacco and *Bryophyllum* treated with substances such as glycine, glutamic acid, 1-cystine, cysteine hydrochlorate, glutathione, thiophenol, parathiocresol, thioglycollic acid, produce scars and swellings of the treated area, which had been previously injured. The swellings are larger than those induced in control specimens by merely injuring them. There is no specific difference in the reactions on plants produced by the compounds bearing the -SH group and those without it. Glutathione and glutamic acid treated stems consistently showed greater reaction.

4. An histological study of the swellings of these stems produced by injury and chemical treatment shows that the reaction tissue is limited in quantity and its location is generally peripheral to the injury. In the injured stems of the controls, the type of reaction is the same but quantitatively smaller; while in the crown gall the actively growing tissue is abundant and is located on the periphery of the gall. The same types of tissues are found in all three cases but the difference lies in the rate of division, differentiation and ageing. Comparatively, crown gall cells divide rapidly, and differentiate and age slowly. Cells of reaction tissue induced by injuries with chemical treatments divide slowly but differentiate and age rapidly. When these tissues are contrasted with the behavior of cancer we find the latter divides rapidly and indefinitely, differentiates slowly and imperfectly and is frequently superseded by necrosis.

5. Chemically induced reaction tissues, when compared with other hyperplasias of plants and animals, are the smallest and simplest types of overgrowths which never reach the malignant stage. In crown gall, tissue

proliferation is more abundant than that induced by injury and chemical stimulation, but limited when compared with neoplastic disease of animals and man. It appears that while the chemical stimulants now known induce greater reactions than the controls, the plant's protective mechanism seems to inhibit continued responses to continued applications of the same stimulus. The isolation of the chemical agent that is responsible for growth stimulation and improved methods of applying this stimulus may eventually overcome this inhibition so that the artificial application of this substance may result in overgrowths in plants, similar to crown gall, club root, potato wart, cedar apple, and galls produced by insects or nematode infestations. The nature of the response seems to be a function of the host rather than of the stimulus.

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Explanation of plate 7

Fig. 1. A, B. Sunflower stems, growing region painted weekly, after injury, with coal tar suspended in ether. Begun 6.10.33 and terminated 8.7.33. $\times \frac{1}{3}$.

Fig. 2. A. Sunflower stem, noninjured, painted weekly from 6.10.33 to 7.6.33. B. Sunflower stem painted after injury with scharlach R and ether. Treatment below growing region of stem. $\times \frac{1}{3}$.

Fig. 3. A. Sunflower stem, control, injured and painted weekly in growing region with ether from 6.24.33 to 8.7.33. $\times \frac{1}{3}$. B. Sunflower stem injured and painted below growing region with coal tar suspended in pentane. $\times \frac{1}{3}$.

Fig. 4. Longitudinal section of uninjured stem painted with coal tar in ether. Compare with figure 1. $\times \frac{1}{3}$.

Fig. 5. Sunflower stem painted once weekly for one month with coal tar in ether, no injury. $\times \frac{1}{3}$.



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Explanation of plate 8

Photographs on this plate were reduced one quarter normal size.

Sunflower stems

1. Treated with glutamic acid. 7.17.34. Removed and photographed 8.10.34. Longitudinal section.
2. Note intumescences after treatment with glutamic acid; photographed 8.27.34.
3. New growth emerging from injured area after treatment with glycine; photographed 8.27.34.
4. Longitudinal section of stem after similar treatment.
5. Swellings about injury after treatment with 1-cystine, 7.17.34; photographed 8.9.34.
6. Longitudinal section of stem; overgrowths about injured area.
7. Injured and treated with parathiocresol; photographed one month later.
8. As in 7, showing irregular nodular masses about area of treatment.
9. Stem treated with glutathione on 7.17.34; photographed 8.10.34.
10. Longitudinal section of stem after similar treatment.
11. Stem after injured area was treated with cysteine hydrochlorate on 7.17.34; photographed 8.27.34.
12. Longitudinal section of another stem, similarly treated; photographed 8.27.34.
13. Stem of control sunflower injured; showing swellings about injuries.
14. Injured stem; control, slight swelling, marked necrosis.
15. Longitudinal section of *N. tabacum* after 18 paintings with coal tar suspended in ether. Paintings began 7.12.33. Last painting 9.2.33; photographed 10.12.33.

Tomato stems

16. Treated with 10% dibenzanthracene in olive oil, after 2 months.
17. Two months after inoculation with a virulent strain of *B. tumefaciens*.

Ricinus communis stems

18. Two months after treatment with .001% dibenzanthracene in olive oil.
19. Longitudinal section of stem after treatment with .01% dibenzanthracene.
20. After treatment with .01% dibenzanthracene.
21. Injured and treated with coal tar suspended in pentane. 6.24.33; photographed 11.4.33.
22. Control; injured and treated with ether only; photographed 17 weeks later.

Datura stramonium stems

23. After 18 paintings with scharlach R in ether; 7.10.33 to 9.2.33; photographed 10.1.33.
24. After injection with 4% coal tar in ether; 8.2.33; photographed 10.1.33.



Explanation of plate 9

Figures on this plate were made with the Carl Zeiss 35 cm. photomicrocamera. The combination of lenses used is as follows: Obj. 10. Oc. 3. Bellows 75 cm. Estimated magnification $\times 90$. K_2 filter was used with W.W. panchromatic M plates.

Fig. 1. Sunflower stem, control, five weeks after injury.

Fig. 2. From scar and pith of tobacco stem painted with coal tar in ether 17 times. (Begun 7.12.33; last painting 9.2.33). Note embryonic rootlike structure imbedded in parenchymatous tissue.

Fig. 3. Sunflower stem near growing point injured and painted with coal tar suspended in ether (10 paintings; 6.17.33 to 8.23.33).

Fig. 4. Sunflower stem crown gall tissue 49 days after inoculation with a virulent strain of *B. tumefaciens*.

Fig. 5. Sunflower stem 10 days after injury and treatment with tryptophane.

Fig. 6. Sunflower stem 40 days after injury and treatment with glutathione.

Fig. 7. Tomato stem painted with scharlach R in ether, four times; 7.12.33 to 7.19.33.



LEVINE CHEMICAL AGENTS

A new *Sedum* from Texas

EDWARD J. ALEXANDER

For the past three years the writer has had under observation at the New York Botanical Garden plants of a *Sedum* received from Mr. A. R. Davis of Marathon, Texas, communicated through Mr. Leon Croizat.

At first sight the plant did not appear like any species ever known to us, but is seemed advisable to grow it through several flowering seasons for checking. After three seasons there seems no further doubt as to its being an undescribed species, not closely related to any known in North America. The writer therefore proposes the name

***Sedum Robertsianum* sp. nov.** Sect. *Seda* genuina (Eusedum) § *Diversifolia*. Planta caespitosa, ramis a basi numerosis decumbentibus 8–12 cm. longis anno secundo florentibus, in parte erecta bifurcata, interdum simplicibus; foliis alternis glabris turgidis ovoideis, 3–4 mm. diam., 5–8 mm. longis, apiculatis; floribus solitariis supraxillaribus in parte caulis erecta 5-(rarissime 4-) meris; sepalis 2 externis quam interioribus multo majoribus, quam petalis dimidio brevioribus; petalis 4 mm. longis lanceolatis flavis, secus lineam medium usque ultra medium canaliculatis, ultra medium foveolatis; staminibus petalis oppositis primum reflexis et in canaliculis accumbentibus, demum erectis.

Type collected by A. R. Davis in Brewster Co., Texas, growing at about 4000 feet elevation on a mountain top in shallow calcareous soil. Description made from plants growing under cultivation at the New York Botanical Garden.

The species is named after Mrs. Kate Roberts, upon whose ranch the original plants were collected. Mr. Davis writes: "The plants are found in lime formation nearly always on top of the highest point of the mountain and in very shallow soil. It is never found low down or in the valley so far as I have been able to determine. It is native to Brewster Co., Texas, and distributed pretty well all over the county."

An erect-sprawling succulent, perennating by short winter shoots which elongate into flowering stems the following year. The leaves on the winter shoots are somewhat imbricated, few in number compared with related species, narrowly ovate, obtusish. The fleshy stems are strongly red-streaked and spotted. The leaves at first are flattened on the ventral side especially towards the tip, the leaf becoming very turgid when fully mature, and broadly elliptical in cross section, except for keels on the sides near the tip. The mature leaves are ovoid, glabrous, yellow-green heavily spotted with red when grown in sun, 5–8 mm. long, and 3–4 mm. in diameter at the point of greatest thickness, the tip obtusely apiculate, slightly upturned. Those on the inflorescence are somewhat smaller, more pointed and less

rotund. The leaves, even under a hand lens, appear minutely papillose, but under the microscope it will be seen that this is an optical illusion caused by the reflections from the inner facets of windowed cells of red, green, and transparent color. The inflorescence is two-branched or sometimes simple, apparently through suppression of other branches, as indicated by short side branches on some inflorescences near the base, which bear one leaf and a single flower. The bright yellow flowers are about 1 cm. across,

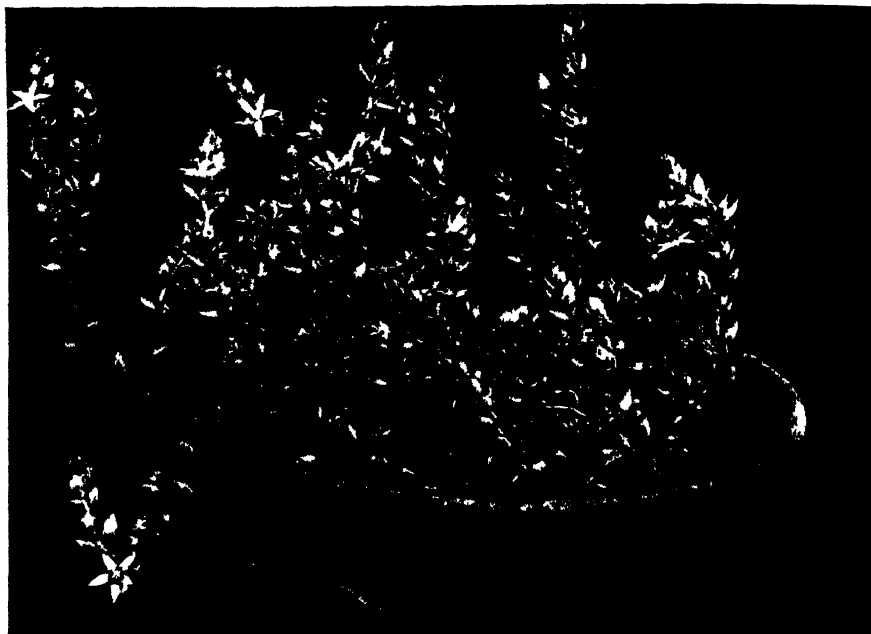


Fig. 1. *Sedum Robertsianum* Alexander, $\frac{2}{3}$ natural size.

equilaterally arranged, and are, even to the lowest, supra-axillary, each very short-stalked or sessile, and having normally a much smaller leaf-like bract not immediately subtending it. On normally developed inflorescences, each branch bears six to twelve flowers. The two outer sepals are much larger than the three inner (in four-parted flowers two large and two small), all lanceolate, the larger half the length of the petals, the smaller half that size. The petals are narrowly lanceolate, about 4 mm. long, greenish at the base, bright yellow above, channelled on the upper surface, the channel deepening into an elliptical pit at a point about two-thirds way up, the pit protruding as a shallow knob on the under surface. When the flower opens, the five stamens alternate with the petals are erect, the five opposite the petals are reflexed, the anthers resting in the pits, and after

anthesis of the calycular series, the corollar series becomes erect and sheds its pollen, after which all ten reflex. The four or five carpels are erect at anthesis, afterwards slowly spreading. The body is oblong-conical, the tips subulate, about one-fourth the length of the body. The mature fruit has not yet been seen.

This species is unique among true sedums in its inflorescence and leaves. In view of its known area of occurrence it should be looked for in the neighboring section of Mexico.

In common with certain others of the genus, the leaves, which are easily detached, will, if left undisturbed, sprout from the severed base within a few days, thus forming an easy method of propagation.

NEW YORK BOTANICAL GARDEN

A method of cultivating myxomycete plasmodia

W. G. CAMP

(WITH FIVE FIGURES)

Methods of cultivating slime mold plasmodia for research and instructional purposes have long been a subject of major interest in research laboratories and in schools. A review of the literature on the use of nutrient substrata for such cultures has been given by Howard (1931) and he has reported the successful culturing of plasmodia on oat agar. The writer has employed Howard's method and has found it successful, but after some experimentation has devised another method of growing plasmodia by feeding them rolled oats without using an agar base. The advantages of the method here described obtain from the facts that relatively enormous quantities of plasmodia can be produced in a single culture with little labor and care, the plasmodia can be easily separated from the material of the substratum, and given cultures can be maintained for a relatively long time and fed periodically.

The material used in this work was obtained as a deep yellow sclerotium formed by the desiccation of a lemon yellow plasmodium in the laboratory. Cultures were first grown from fragments of the sclerotium in petri dishes on oat agar. In the course of time some of the cultures formed sporangia and the form was identified as *Physarum polycephalum* Schw.

The method of culturing which has been developed is as follows: the upper surface of a Petri dish is covered with gauze or filter paper and the edges are folded under the rim of the dish. This is placed, inner face down, in a battery jar or similar vessel containing water to a depth of about one centimeter and which can be covered with a glass plate. Living plasmodial or sclerotial fragments are placed on the gauze or filter paper where capillary water affords moisture for the substratum. Water in the battery jar must not be of such depth that the gauze or paper is flooded. The plasmodia so far observed appear to be very markedly aerobic, and a substratum flooded with water is not conducive to good growth and activity. When a piece of living plasmodium is placed on the moist surface, it will very soon begin to creep and spread over this surface (fig. 1) and if a sclerotium is placed there, an active plasmodium emerges in a few hours (fig. 4). In either case, after the plasmodium has spread over a portion of the moist surface, feeding may begin. This is provided for by sprinkling a small amount of pulverized rolled oats directly on the plasmodium (fig. 2). The plasmodium creeps up around the oat particles and appears to feed by ingesting and surrounding them directly (fig. 3). When starting a culture care must be exercised against using an excessive quantity of crushed

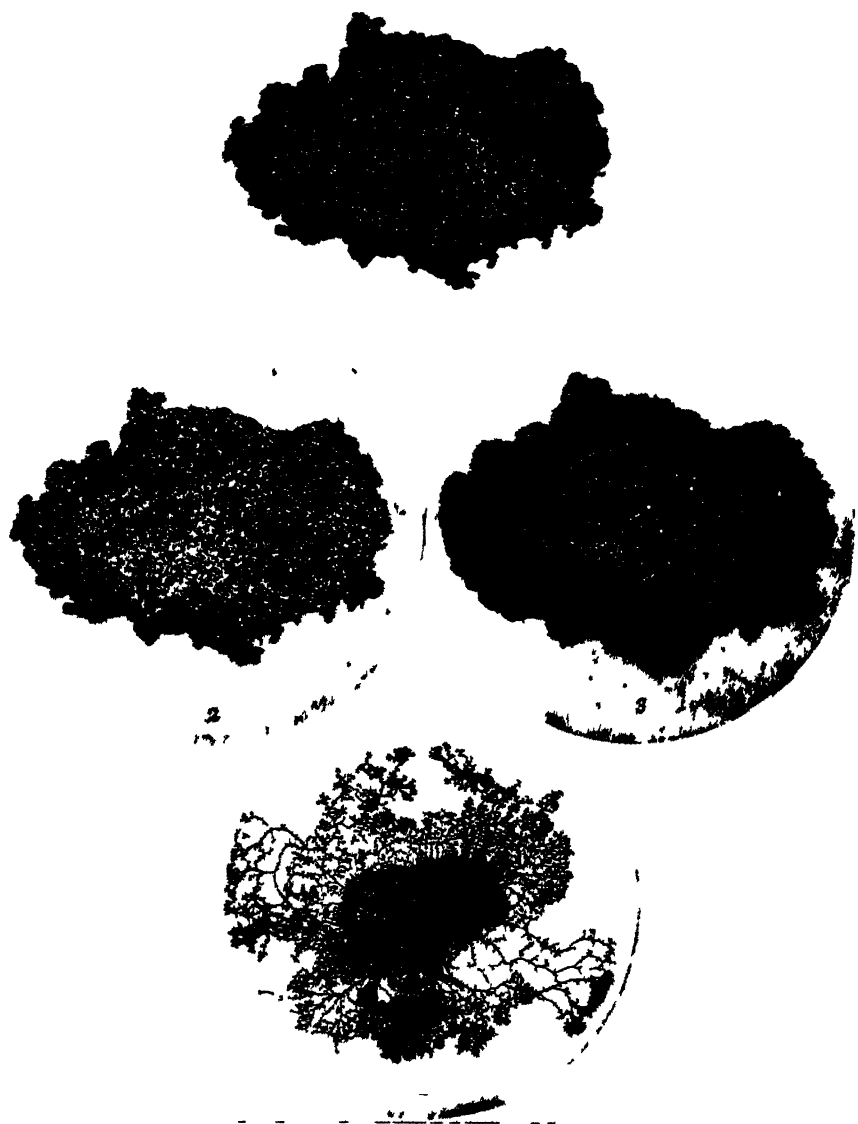


Fig. 1. Plasmodium spread over moist substratum.

Fig. 2. The same plasmodium as in figure 1 with pulverized rolled oats sprinkled over its surface.

Fig. 3. The same plasmodium as above thirty minutes later. The plasmodium has surrounded most of the oat particles.

Fig. 4. Plasmodium which emerged from a sclerotium (dark mass in the center of the photograph).

oats, and a little experience at this stage of culturing soon enables one to determine the quantity that should be used. An excessive quantity placed over the plasmodium or on areas of the moist substratum not occupied by the plasmodium tends to promote bacterial and fungus growth, and the culture may suffer from the growth of these other organisms. Following the initial feeding stage the plasmodium grows and spreads over a wider and wider area and finally is distributed over the whole moist surface. In the early stages of culturing, feeding is repeated as often as the plasmodium completely surrounds all of the oat particles from the previous feeding. Finally a very luxuriant plasmodium covers the whole surface of the substratum and at each subsequent feeding crushed oats may be sprinkled on the plasmodium until there is a more or less continuous covering layer. Plasmodial strands creep up between the particles of oats, and within the space of a few hours appear to have all of the particles completely surrounded. After the plasmodium attains considerable size, noticeable growth of fungi and bacteria in the nutrient substratum seldom occurs.

As the plasmodium grows, it creeps down the gauze or paper, which extends into the water, until the water level is reached and then across the surface of the water and up and over the inner surface of the culture vessel (fig. 5). To facilitate rapid spread of a plasmodium from the substratum on which it is growing to the wall of the culture vessel, the petri dish supporting the substratum is placed flush against the wall of the vessel. This direct contact obviates the necessity of the plasmodium creeping over the surface of the water, and almost invariably plasmodia tend to follow the bridge thus provided rather than creep over the water surface. Where the plasmodium comes in contact with water, it produces a copious amount of slime which has the appearance and consistency of egg white, but on dry surfaces or surfaces which are only slightly moist, a comparatively small amount of slime is produced.

When a culture is once well established, by following the method described, it requires on the average, no more than a few minutes of attention each day to gather the plasmodium from the walls of the culture vessel, remove the Petri dish so as to be able to wash the vessel, feed that portion of the plasmodium which remains on the supporting substratum and set the culture up for another daily period of growth and expansion. The writer has maintained cultures set up in this way for periods longer than two months, and from each culture has gathered relatively enormous quantities of protoplasm freed of all of the material of the substratum. The living plasmodia may be gathered from the walls of the vessels in various ways. At times plasmodia form dense compact masses covering an area ranging from a few to several square centimeters, which masses

may become several millimeters thick. Accumulations of this type may be harvested by removal with a broad flat instrument such as a section litter or spatula. Again the plasmodia may distribute themselves as thin reticula over the surface of the glass. A reticulum may be gathered by first removing the petri dish with its covering of nutrient substratum, then washing the reticulum from the wall of the vessel with a small stream of water, and finally lifting the clumps and strands of protoplasm from the water or separating them from the water by filtering. A third method of



Fig 5. Plasmodium which has spread from the substratum to the inner surface of the culture vessel

gathering plasmodia which is very easy and labor saving if one wishes to produce sclerotia, is to line the inner sides of the culture vessels with sheets of paper of appropriate size. Almost any kind of paper is satisfactory but a smooth paper is preferred as compared to paper with a rough or corrugated surface. Plasmodia creep on to and over the paper and at an appropriate time the sheets themselves are removed from the culture vessels with the protoplasmic reticula spread over and clinging to their surfaces.

The habit of some of the *Myxomycetes* of forming sclerotia and the general conditions under which sclerotial formation takes place have long

been known. This habit can be utilized advantageously in preserving viable material and obviates the necessity of maintaining living cultures of plasmodia for future use. The writer obtains sclerotial formation by slow desiccation of plasmodia on paper. This desiccation is accomplished at room temperature by placing plasmodia on sheets of paper under bell jars and providing a very small opening so that slow exchange of gases can take place between the atmosphere of the bell jar and the external atmosphere. The optimum conditions for sclerotization have not been determined but if desiccation is too rapid, the plasmodia form horny non-viable masses. It is effective to extend the period of desiccation over a twenty-four hour period. During sclerotization the protoplasm of a plasmodium forms one or more compact masses which may vary in thickness up to more than five millimeters but with continued desiccation this thickness usually decreases to less than two millimeters. The fully formed sclerotia whose color may vary from brilliant lemon yellow to light brown may be removed from the paper on which they are formed and preserved at ordinary temperatures. They have remained viable after exposure to the temperature of liquid air for ten minutes and after exposure to a temperature of 52°C. for two weeks. Furthermore, fragmentation of sclerotia does not destroy their viability. A finely ground mass obtained by pulverizing a sclerotium produces an active plasmodium at room temperature when afforded the proper conditions of moisture.

The utility of culturing myxomycete plasmodia by such a method as has been described is at once suggested. Unlimited quantities of naked protoplasm can be obtained for use in chemical and physical research studies. Comparatively few such studies on the plasmodia of slime molds have been made, which fact has undoubtedly been due to the difficulty of obtaining sufficient quantities of material. It is worth noting that in the chemical studies of Walter (1921), Lepeschkin (1923), Kiesel (1925, 1927) and Iwanoff (1925), the materials used were collected from substrata upon which slime molds naturally occur. The difficulties and limitations of collecting plasmodia from their natural substrata for use in such studies are obvious. Furthermore, this method of culturing is adapted to experiments such as those which demonstrate the relationship of hormones, vitamins and auxins as well as the better known constituents of dietary substances to growth and development. Such experiments should be more fundamentally significant than similar experiments with the embryonic and later developmental stages in the higher plants and animals on the one hand and with tissue cultures on the other hand. A plasmodium is relatively free of the complexities of organismal differentiation characteristic of the higher plants and animals, yet it feeds and grows and reaches

reproductive maturity. In this latter respect it is fundamentally different from ordinary cultures of isolated tissues such as those of Carrel (1912) and Ebeling (1921) for animal tissues, and those of Robbins (1922) and White (1934) for plant roots and stems.

The procedures here described have been applied extensively to only one species of slime mold, namely, *Physarum polycephalum*. Experiments with other forms are being made and more exact quantitative data as to nutrient materials, temperature, moisture, light and other relations will be obtained.

The writer is indebted to Dr. R. A. Harper and to Dr. J. S. Karling for assistance in the preparation of the manuscript.

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A revision of the genus *Axinaea* (Melastomaceae)¹

DONALD S. EVES

The genus *Axinaea* was proposed and first described by Ruiz and Pavon (Prodr. 68. 1794). This description was based upon *A. lanceolata* Ruiz & Pav. and *A. purpurea* Ruiz & Pav. *A. purpurea*, however, was transferred at a later date to the genus *Meriania* as *M. purpurea* (Ruiz & Pav.) Sw. (Fl. Ind. Occ. 2: 829). DeCandolle (Prodr. III: 102. 1828) described the genus *Chastenea*, which he considered to be closely related to *Axinaea* and distinguished from it by a truncate and entire calyx-limb, one-pored anthers, and rotund connectives. Naudin (Ann. Sci. Nat. III. 18: 120. 1852) regarded *Axinaea* as a doubtful genus. He transferred some of its species to *Chastenea*, and questioned the remaining ones as being dubiously placed. These questionable species were later transferred to other genera by other workers. Triana (Trans. Linn. Soc. Bot. 28: 69. 1871) re-introduced the name *Axinaea* to take the place of *Chastenea*, considering it to be the valid one because of priority in use. *Axinaea* species have sometimes been confused with *Meriania* species, and transfers have been made from one genus to the other in both directions. In this paper twenty-two species are included in the genus *Axinaea*, one of which is new.

The taxonomic position of *Axinaea* is in the tribe Merianieae of the family Melastomaceae. The genus is most closely related to *Meriania*, from which it differs principally in the character of the anther-connectives: in *Axinaea* these have a thick and often inflated appendage in the rear; whereas in *Meriania* they have a blunt or pointed projecting spur at the base in the rear, and often a second spur ascending parallel to the anther-sacs and situated above the first spur.

This study, conducted at the Britton Herbarium, was undertaken at the suggestion of Dr. H. A. Gleason, to whom I am especially indebted for guidance and assistance during the course of this undertaking. I also wish to thank the following institutions for their courtesy in lending herbarium specimens: The Conservatoire Botanique, Geneva (G), the Botanisches Museum, Berlin (B), the Royal Botanical Gardens, Kew (K), the Field Museum, Chicago (F), and the New York Botanical Garden, New York (Y). The initials in parentheses are those used in the taxonomic treatment below to designate the location of cited specimens in the various herbaria.

DISCUSSION OF THE GENUS

AXINAEA Ruiz & Pav. Prodr. 68. 1794.

¹ Submitted in partial fulfillment of the requirements for the degree of Master of Arts in the Faculty of Pure Science. Columbia University.

Chastenea DC. Prodr. III. 102. 1828.

Flowers 5-merous (4-merous in *A. crassinoda* Triana); hypanthium hemispheric, campanulate, or cyathiform, glabrous or furfuraceous; calyx-limb truncate or shortly and broadly lobed; petals commonly obovate, occasionally oblong or suborbicular, rounded, retuse, or apiculate, usually slightly asymmetrical, imbricate in the campanulate corolla; stamens 10, equal or subequal; filaments glabrous, flattened, broad; anther-sacs straight or slightly arcuate, linear-subulate, minutely 1-pored at the apex; connectives vesiculate, inflated and appendiculate in the rear, sometimes radially flattened; style filiform or robust, erect or arcuately declined, sometimes abruptly curved at the top; stigma truncate or attenuate; ovary free, glabrous, 5-celled, subcylindrical, ovoid, or obovoid, 5-lobed at the apex; fruit a capsule included in the hypanthium or with the apex exserted, 5-valved; seeds many, oblong-pyramidal.

Shrubs and trees; branchlets terete or tetragonal, sometimes greatly swollen at the nodes or with prominent stipule-scars, glabrous or pubescent; leaves opposite, ovate, elliptical, or oblong, acute, obtuse, or apiculate at the apex, cordate, auriculate, or subrounded to attenuate at the base, the basal margins often shortly revolute-decurrent, petioled (scarcely so or not at all in *A. sessilifolia* Triana), entire or sinuately toothed, 5-9-nerved, sometimes plinerved, glabrous or pubescent beneath, coriaceous (scarcely so or even membranaceous in a few species); petiole slender or stout, glabrous or pubescent, sometimes dilated at the apex with the lower leaf-margins confluent over it to form a transverse tubercled scutum; stipules deciduous (persistent in a few species); flowers large, white, rose, red, or purple, in broad terminal or axillary panicles.—Twenty-one species of tropical Andean South America from Venezuela to Bolivia, and one species from Costa Rica.

The type species is *A. lanceolata* Ruiz & Pav.

KEY TO THE SPECIES

- a. Stipules persistent, or stipule-scars prominent as thickened rings b.
 - b. Leaf-base cordate c.
 - c. Leaves sessile or very nearly so. 1. *A. sessilifolia*
 - c. Leaves conspicuously petioled. 2. *A. crassinoda*
 - b. Leaf-base not cordate d.
 - d. Branchlets conspicuously tetragonal, greatly swollen at the nodes. 16. *A. robusta*
 - d. Branchlets obscurely tetragonal, scarcely swollen at the nodes e.
 - e. Petiolar-scutum present; leaves 5-7-nerved. 17. *A. costaricensis*
 - e. Petiolar-scutum absent; leaves 5-pli-nerved. 10. *A. dependens*
- a. Stipules deciduous, stipule-scars not prominent as thickened rings f.
 - f. Leaves densely ferruginous-tomentose beneath g.
 - g. Tomentum of leaves furfuraceous or shortly stellate; leaf-base usually auriculate, with the auricles sometimes reflexed h.
 - h. Branchlets obscurely tetragonal or terete. 3. *A. glandulosa*
 - h. Branchlets acutely tetragonal. 4. *A. Weberbaueri*
 - g. Tomentum of leaves elongate and plumose; leaf-base acute i.
 - i. Petals less than 15 mm. long; hypanthium 7 mm. wide; petiolar-scutum present but sometimes much reduced. 5. *A. tomentosa*

- i. Petals more than 20 mm. long; hypanthium 12 mm. wide; petiolar-scutum absent. 6. *A. sclerophylla*
- f. Leaves glabrous or merely somewhat furfuraceous beneath (whitish-arachnoid in *A. lepidota*) j.
- j. Branchlets and lower leaf-surfaces whitish-arachnoid, especially when young; upper leaf-surfaces nigrescent when dry; leaves 3-5 cm. long, 3-5-ply-nerved. 22. *A. lepidota*
- j. Branchlets and lower leaf-surfaces never whitish-arachnoid; leaves usually more than 5 cm. long k.
- k. Leaf-base cordate or auriculate, with the lobes sometimes small and reflexed l.
- l. Leaf-margins entire. 14. *A. Lehmannii*
- l. Leaf-margins toothed m.
- m. Petiolar-scutum absent; branchlets sharply tetragonal. 7. *A. lanceolata*
- m. Petiolar-scutum present; branchlets obscurely tetragonal n.
- n. Branchlets and lower leaf-surfaces glabrous; petiolar-scutum conspicuous as a distinct sheath. 8. *A. scutigera*
- n. Branchlets and lower leaf-surfaces thinly furfuraceous; petiolar-scutum wart-like. 9. *A. Pennellii*
- k. Leaf-base neither cordate nor auriculate, often shortly decurrent, with the decurrent part sometimes expanded and recurved o.
- o. Leaves 5-ply-nerved, sometimes only slightly so p.
- p. Leaf-margins toothed, at least distally. 21. *A. Merianiae*
- p. Leaf-margins entire q.
- q. Leaves 15-30 cm. long. 11. *A. Drakei*
- q. Leaves 6-14 cm. long r.
- r. Petioles 1 cm. long; panicles few-flowered. 12. *A. pauciflora*
- r. Petioles 2-4 cm. long; panicles many-flowered. 13. *A. speciosa*
- o. Leaves 5-7-nerved s.
- s. Petiolar-scutum present t.
- t. Branchlets dark and conspicuously lustrous; leaf-base not at all decurrent. 15. *A. nitida*
- t. Branchlets not dark and conspicuously lustrous; leaf-base usually shortly decurrent, with the decurrent part recurved or expanded and crisped. 18. *A. grandifolia*
- s. Petiolar-scutum absent u.
- u. Submarginal veins the 6th and 7th; leaves 7-12 cm. long. 19. *A. macrophylla*
- u. Submarginal veins the 4th and 5th; leaves 4-5 cm. long. 20. *A. affinis*

TREATMENT OF THE SPECIES

1. AXINAEAE SESSILIFOLIA Triana, Trans. Linn. Soc. Bot. 28: 69. 1871.

Branchlets tetragonal, keeled on the angles, greatly swollen at the nodes, with stipules persistent or stipule-scars prominent, glabrous; leaves *sessile or very nearly so*, elliptical-oblong, 15-20 cm. long, 6-10 cm. wide, obtuse at the apex, cordate at the base, entire, 5-7-ply-nerved, conspicuously reticulate, glabrous above and beneath, membranaceous; panicles pendulous, widely branched; pedicels glabrous, 8-10 mm. long; hypanthium cyathiform, glabrous, 8 mm. wide; calyx-limb subtruncate; petals oblong, rounded or barely retuse, 13 mm. long; filaments 6 mm. long; anther-sacs long-attenuate, 10 mm. long; connectives with large prominent dorsal lobe against the anther-sacs, apiculate, 4 mm. long; style abruptly curved near the tip, 8-9 mm. long.

ECUADOR—Chimborazo: *Spruce 6174*, type collection (K).

A. sessilifolia is a tree about 12 m. tall. The petals are blood-red and the anthers yellow. This species can be readily distinguished from the others of the genus by its sessile (or very nearly so) leaves. It is perhaps most closely related to *A. crassinoda*.

2. AXINAEA CRASSINODA Triana, Trans. Linn. Soc. Bot. 28: 69. 1871.

Branchlets more or less tetragonal, *greatly swollen at the nodes*, with stipules persistent or stipule-scars very prominent, densely to thinly hirsute-pubescent; petioles stout, densely scurfy to hirsute, 4–7 cm. long, without a scutum; leaves broadly ovate, 13–19 cm. long, 12–16 cm. wide, obtuse and rounded at the apex, *cordate at the base, conspicuously crenate-dentate*, 7–9-nerved, conspicuously reticulate beneath, glabrous above, scurfy on the nerves and veinlets beneath, subcoriaceous; panicles pendulous, with spreading branches, about 16 cm. long; pedicels furfuraceous, 4–10 mm. long; hypanthium broadly cyathiform, finely furfuraceous, 7 mm. wide; calyx-limb broadly 4-lobed to truncate; petals 4, obovate, retuse, 8–10 mm. long; stamens 8; filaments 3–4 mm. long; anther-sacs 5 mm. long; connectives conic, acuminate, 4 mm. long; style slightly curved, 9–12 mm. long.

PERU—Prov. of Chachapoyas: *Mathews 3213*, type (K); Playampampa: *Macbride 4873* (F).

A. crassinoda is the only species of the genus having tetramerous flowers. It is most closely related to *A. sessilifolia*.

3. AXINAEA GLANDULOSA Ruiz & Pav. Fl. Per. 4: t. 412. 1802.

Chastenea glandulosa (Ruiz & Pav.) Naud., Ann. Sci. Nat. III. 18: 123, 124. 1852.

Branchlets obscurely tetragonal, slightly swollen at the nodes but with stipule-scars not prominent, furfuraceous near the tips; petioles robust, somewhat furfuraceous, 2–4 cm. long, *with a conspicuous scutum*; leaves ovate, 10–15 cm. long, 5–7 cm. wide, acute at the apex, *auriculate at the base, with the auricles reflexed*, entire or very minutely sinuate-denticulate, 5–7-nerved, glabrous above, *densely furfuraceous-tomentose beneath*, coriaceous; panicles erect, stoutly peduncled; pedicels thick, furfuraceous, 5–8 mm. long; hypanthium broadly campanulate, glabrous, rugose, 7 mm. wide; calyx-limb subtruncate; petals oblong-obovate, apiculate, 13 mm. long; filaments curved, 4–5 mm. long; anther-sacs 6 mm. long; connectives broadly ovate, flattened, obtuse or acute, 3 mm. long by 2½ mm. broad; style subfiliform, 15 mm. long.

PERU—Chinchao: *Ruiz s. n.*, type collection (B, K); near Pampayaca: *Kanehira 11* (F).

A. glandulosa has white flowers. The species is most closely related to *A. Weberbaueri*. It differs especially, however, in having obscurely tetrag-

onal and branchlets and the basal lobes of the leaf conspicuously reflexed. It is probably also related to *A. tomentosa*. The Ruiz collection from Chinchao and deposited at the Botanisches Museum has been considered by some to be the type collection of *A. lanceolata*. I am persuaded to agree with Markgraf, however, that the specimen represents *A. glandulosa*. It differs from *A. lanceolata* in having the leaves densely tomentose beneath, obscurely tetragonal branchlets, and a petiolar-scutum.

4. AXINAEA WEBERBAUERI Cogn., Engl. Bot. Jahrb. 50: Beibl. III. 32. 1913.

Branchlets *acutely tetragonal*, slightly swollen at the nodes, furfuraceous-puberulent; petioles slender, furfuraceous, $1\frac{1}{2}$ –4 cm. long, with a small tubercle-like scutum; leaves narrowly ovate or ovate-lanceolate, 8–18 cm. long, 3–8 cm. wide, acuminate at the apex, obtuse or *generally small auriculate* at the base, minutely and remotely denticulate, 5-nerved, glabrous or sometimes furfuraceous-puberulent at the base above, *shortly and densely stellate-tomentose beneath*, coriaceous; panicles erect, densely many-flowered, about 5–8 cm. long; pedicels densely furfuraceous, 2–6 mm. long; hypanthium broadly campanulate, glabrous above, furfuraceous-puberulent at the base, 8 mm. wide; calyx-limb subtruncate; petals obovate to oblong, retuse, 10–16 mm. long; filaments $4\frac{1}{2}$ mm. long; anther-sacs flattened, with two lateral wings running down from the connectives, 6 mm. long; connectives ovoid, acute or obtuse, 3 mm. long; style slender, sometimes abruptly curved at the top, 6–15 mm. long.

PERU—Prov. of Huanta: *Weberbauer 5648*, type (B), isotype (F).

A. Weberbaueri is a tree about 4 m. tall, occurring at an altitude of 2700–3000 m. The leaves are intensely green above and green to ashy beneath. The petals are violet or purple. This species is most closely related to *A. glandulosa*, from which it differs especially in having acutely tetragonal branchlets and the basal lobes of the leaf somewhat recurved but not conspicuously reflexed.

5. AXINAEA TOMENTOSA Cogn. DC. Monogr. Phan. 7: 451. 1891.

Branchlets conspicuously tetragonal, slightly swollen at the nodes, with stipule-scars more or less obscure, furfuraceous; petioles stout, furfuraceous, 2– $3\frac{1}{2}$ cm. long, *with a scutum present* but sometimes much reduced; leaves broadly elliptical, 12–15 cm. long, $7\frac{1}{2}$ –8 cm. wide, apiculate to obtusely acuminate at the apex, acute and slightly revolute at the base, finely and remotely denticulate, 5–7-nerved, often slightly pli-nerved, glabrous above, *densely rusty-tomentose with plumose hairs beneath*, coriaceous; panicles erect, compact, many-flowered, about 9 cm. long; pedicels densely furfuraceous-puberulent, thick, 2–5 mm. long; hypanthium broadly campanulate, furfuraceous, 7–8 mm. wide; calyx-limb truncate to shallowly 5-lobed; petals obovate to oblong, obtuse to subretuse, 12–15 mm. long; filaments flattened-filiform, 6–8 mm. long;

anther-sacs 6–8 mm. long; connectives ovoid, with two large and somewhat flattened lateral lobes, blunt, 3 mm. long by 4 mm. broad; style slender, 17 mm. long.

PERU—Chachapoyas: *Mathews s. n.*, isotypes (Y, K, B); Prov. of Bongara: *Weberbauer 7150* (F, B).

A. tomentosa is a shrub about 4 m. tall, occurring at an altitude of 2500–2600 m. This species is most closely related to *A. sclerophylla*, from which it may be distinguished by the presence of a petiolar-scutum, a hypanthium 7–8 mm. wide, and petals usually less than 15 mm. long.

6. *AXINAEA SCLEROPHYLLA* Triana, Trans. Linn. Soc. Bot. 28: 68. 1871.

Branchlets conspicuously tetragonal, swollen at the nodes, without stipule-scars, tomentose; petioles robust, tomentose, 2–3 cm. long, *without a scutum*; leaves broadly elliptical, 12–15 cm. long, 7–9 cm. wide, shortly and obliquely round-acuminate at the apex, with the acumen recurved, subacute at the base, with the basal margin slightly expanded and reflexed, remotely serrate on the upper half or entire, 5-plex-nerved, glabrous above, *densely rusty-tomentose with elongate plumose hairs beneath*, coriaceous; panicles axillary, few-flowered, cymose; pedicels stout, furfuraceous, 2–3 mm. long; hypanthium hemispheric, tomentose at the base, 12 mm. wide; calyx-limb truncate; petals broadly obovate, retuse, 22 mm. long; filaments 11 mm. long; anther-sacs subulate, 7–8 mm. long; connectives ovoid, somewhat flattened, blunt, 4 mm. long; style stout, curved at the top, 14 mm. long.

ECUADOR—region of Loja: *Seemann s.n.*, type (K).

A. sclerophylla is most closely related to *A. tomentosa*, and the two superficially resemble one another. The former, however, is characterized by petals commonly more than 20 mm. long, a hypanthium about 12 mm. wide, and the presence of a petiolar-scutum.

7. *AXINAEA LANCEOLATA* Ruiz & Pav. Fl. Per. 4: t. 409. 1802.

Chastenea lanceolata (Ruiz & Pav.) Naud., Ann. Sci. Nat. III. 18: 123. 1852.

Branchlets *acutely tetragonal*, subglabrous; petioles slender, subglabrous, 5–6 cm. long, *without a scutum*; leaves ovate-lanceolate, 10–20 cm. long, 3–10 cm. wide, bluntly acuminate at the apex, auriculate at the base, *with the auricles conspicuously folded under*, remotely serrate, 5–7-nerved, glabrous above, subglabrous beneath, coriaceous; panicles pendulous, few-flowered, small; pedicels furfuraceous or glabrous, 5–10 mm. long; hypanthium broadly campanulate, granular-pubescent or glabrous, 6–11 mm. wide; calyx-limb subtruncate; petals oblong to obovate, rounded or retuse, 10–18 mm. long; filaments 3–5 mm. long; anther-sacs subulate, 5–8 mm. long; connectives ovoid, obtuse or acute, 3–4 mm. long; style filiform, 5 mm. long.

PERU—Sandillani: *Pearce s.n.* (K). BOLIVIA—Dept. of Cochabamba, Quebrada de Corani: *Steinbach 8861* (Y, B).

A. lanceolata is a shrub or tree up to 18 m. tall, occurring at an altitude of 2400–2700 m. The flowers range in color from pink to white, and blossom in June, July, and August. This species is perhaps most closely related to *A. scutigera*. From the material at hand it would seem that *A. lanceolata* and *A. scutigera* are too widely separated geographically to be very closely related. Nevertheless, these two species appear to be more closely related one to the other than to any of the other species of the genus.

8. AXINAEA SCUTIGERA Triana, Trans. Linn. Soc. Bot. 28: 69. 1871.

Branchlets tetrangular, shining, glabrous; petioles slender, glabrous, 3 cm. long, with a scutum conspicuous as a distinct sheath; leaves ovate, 7–10 cm. long, 4–5 cm. wide, round-acuminate at the apex, cordate at the base, with the basal lobes sometimes reflexed, remotely sinuate-serrate, 7-nerved, conspicuously reticulate, glabrous above and beneath, coriaceous; panicles axillary, compact, irregularly branched; pedicels essentially glabrous, curved, 10 mm. long; hypanthium hemispheric, glabrous, 6 mm. wide; calyx-limb truncate; petals obovate, apiculate, 12–15 mm. long; filaments arcuate, 7 mm. long; anther-sacs subulate, 6 mm. long; connectives ovoid, flattened, blunt, 4 mm. long; style curved, 13 mm. long.

COLOMBIA—Prov. of Antioquia: *Triana s.n.*, type collection (K).

A. scutigera occurs at an altitude of 2500 m. This species is perhaps most closely related to *A. lanceolata*, which it somewhat resembles. It differs principally, however, by its conspicuously sheathing petiolar-scutum.

9. AXINAEA PENNELLI Gleason, Bull. Torr. Club. 54: 28. 1927.

Branchlets subterete, becoming obscurely tetragonal near the tips, somewhat swollen at the nodes, ochre-scurfy near the tips; petioles slender, scarcely scurfy, $1\frac{1}{2}$ –2 cm. long, with a minute wart-like scutum which is sometimes inconspicuous; leaves long-ovate, 10–16 cm. long, $3\frac{1}{2}$ –6 cm. wide, blunt-acuminate at the apex, small auriculate at the base, with the auricles reflexed and overlapping, conspicuously sinuate-serrate, 5–7-nerved, glabrous above, thinly ochraceous-furfuraceous beneath, more or less coriaceous; panicles erect, about 10-flowered; pedicels thinly furfuraceous, 5–10 mm. long; hypanthium broadly hemispheric, glabrous or very thinly furfuraceous, 10 mm. wide; calyx-limb truncate; petals oblong-obcordate, retuse, 16 mm. long; filaments 7–10 mm. long; anther-sacs 6–9 mm. long; connectives ovoid, blunt, 5–6 mm. long; style 14 mm. long.

PERU—forested cliff above Rio Pillahautu: *Pennell 14003*, type (Y), cotype (F).

A. Pennellii is a tree occurring at an altitude of 2300–2400 m. The petals are purple. This species is probably most closely related to *A. lanceolata*, from which it is distinguished by its subterete or obscurely tetragonal branchlets and the presence of a petiolar-scutum.

10. *AXINAEA DEPENDENS* Ruiz & Pav. Fl. Per. 4: t. 411. 1802.

Meriania dependens (Ruiz & Pav.) Naud., Ann. Sci. Nat. III. 18: 124, 129. 1852.

Branchlets obscurely tetragonal, scarcely swollen at the nodes, *with stipules persistent and semi-circular*, finely furfuraceous, becoming glabrous; petiole slender to thickish, furfuraceous-puberulent, $1\frac{1}{2}$ – $4\frac{1}{2}$ cm. long, without a scutum; leaves elliptical-lanceolate, 11–16 cm. long, 3–5 cm. wide, acuminate at the apex, acute to rounded at the base, undulate-denticulate, *5-plexi-nerved*, prominently reticulate beneath, glabrous above, furfuraceous-puberulent beneath, especially so along the nerves, submembranaceous; panicles pendulous, elongate, about 25 cm. long; pedicels puberulent, 10–12 mm. long; hypanthium hemispheric, finely furfuraceous, 5–7 mm. wide; calyx-limb obscurely 5-lobed; petals oblong-obovate, obtuse, 10–12 mm. long; filaments very flat, 5 mm. long; anther-sacs 6 mm. long; connectives narrowly conic, long acuminate, 5 mm. long; style attenuate, 12–18 mm. long.

PERU—Vitoc: *Ruiz s.n.*, type collection (B); Chichao: *Ruiz s.n.* (B), *Lobb s.n.* (K).

In *A. dependens* the leaves are intensely green above and ashy green beneath. It is probably most closely related to *A. lanceolata*, from which it is readily distinguished by the persistent and semi-circular stipules, the acute to rounded leaf-base, and the obscurely tetragonal branchlets. The specimen collected by Ruiz at Chinchao and now deposited at the Botanisches Museum, Berlin, has been considered by some to be the type collection of *A. glandulosa*. I am persuaded to agree with Markgraf, however, that this consideration is in error and that the particular specimen represents *A. dependens*. It differs from *A. glandulosa* in having plexi-nerved leaves, persistent and semi-circular stipules, and no petiolar-scutum.

11. *AXINAEA DRAKEI* Cogn., DC. Monogr. Phan. 7: 447. 1891.

Branchlets robust, somewhat furfuraceous-puberulent; petioles robust, somewhat furfuraceous-puberulent, 2–3 cm. long, without a scutum; leaves ovate-elliptical, *15–30 cm. long*, 8–15 cm. wide, obtuse at the apex, subrounded at the base, *entire*, *5-plexi-nerved*, prominently reticulate beneath, glabrous above, furfuraceous-puberulent beneath, sometimes only so on the nerves, hardly coriaceous; panicles few-flowered, 10–15 cm. long; pedicels thick, short, very much flattened, minutely hirsute, 5–8 mm. long; hypanthium broadly campanulate, more or less furfuraceous-puberulent, 12–13 mm. wide; calyx-

limb subtruncate; petals obliquely obovate, 20 mm. long; filaments 7–8 mm. long; anther-sacs linear, 7–8 mm. long; connectives slightly thickened dorsally, acuminate, style thick, 12–13 mm. long.

ECUADOR—Quebrada near Loja: *Poortmann* in hb. *Drakei*. No specimens of this species were examined.

A. Drakei is a shrub 2–4 m. tall, with robust branches. The leaves are pallid above and dusky beneath. The petals are crimson. No specimens of this species were received from the herbaria from which sheets have been borrowed. The above description is based entirely upon Cogniaux's description as it occurs in DC. Monogr. Phan. 7: 447, 1891. This species is probably most closely related to *A. pauciflora*, from which it is readily distinguished by the large leaves (15–30 cm. long). It may also be closely related to *A. speciosa*.

12. AXINAEA PAUCIFLORA Cogn., DC. Monogr. Phan. 7: 448. 1891.

Branchlets rather slender, obtusely tetragonal, somewhat furfuraceous; petioles robust, more or less furfuraceous-puberulent, 1 cm. long, without a scutum; leaves ovate, 6–9 cm. long, 4–6 cm. wide, obtuse at the apex, subacute at the base, entire, 5-*pli-nerved*, glabrous above, somewhat furfuraceous-puberulent beneath, scarcely coriaceous; panicles terminal, cymose, 5-flowered; pedicels somewhat slender, shortly hirsute, 10 mm. long; hypanthium broadly hemispheric, slightly furfuraceous-puberulent, 8–9 mm. wide; calyx-limb dilated, subentire; filaments 5 mm. long; anther-sacs linear, 5 mm. long; connectives narrowly ovoid, acute; style thick, 15 mm. long.

ECUADOR or PERU—*Grisar* in hb. Mus. Paris. No specimens of this species were examined.

In this species the leaves are pallid green above and ashy-green beneath with robust nerves. No specimens of this species occur among the herbaria sheets that have been borrowed. The description above is based entirely upon that of Cogniaux's in DC. Monogr. Phan. 7: 448, 1891. *A. pauciflora* is probably most closely related to *A. Drakei*. The two may easily be distinguished by the length of the leaf: in the former the leaves are 6–9 cm. long, whereas in the latter they are 15–30 cm. long.

13. AXINAEA SPECIOSA Britt., Bull. Torr. Club 17: 57. 1890.

Branchlets obscurely tetragonal, with stipule-scars not evident, slightly scurfy near the tips; petioles glabrous, 2–3½ cm. long, without a scutum; leaves lanceolate, 10–14 cm. long, 3–6½ cm. wide, obtuse at the apex, subrounded or acute at the base, entire, 5-*pli-nerved*, conspicuously reticulate, glabrous above, slightly brown scurfy to glabrous beneath, coriaceous; panicles densely flowered, about 12 cm. long; pedicels slightly scurfy, 15 mm. long;

hypanthium broadly cyathiform, glabrous, 9 mm. wide; calyx-limb truncate to subtruncate; petals suborbicular, rounded, 15–24 mm. long; filaments 10 mm. long; anther-sacs attenuate, 10 mm. long; connectives conic, with a small prominent dorsal lobe, long acuminate; style filiform, slightly arcuate, 9–12 mm. long.

BOLIVIA—Mapiri: *Rusby* 2328, type (Y), isotypes (F, B); road from Pararani to Mapiri: *Tate* 393 (Y) ; San Carlos: *Buchtien* 1001 (B).

In *A. speciosa* the leaves are dark green above and pallid beneath. This species is probably most closely related to *A. Drakei* or *A. pauciflora*.

14. *AXINAEA LEHMANNII* Cogn., Engl. Bot. Jahrb. 8: 20. 1886.

Branchlets obscurely tetragonal, somewhat swollen at the nodes, without stipule-scars or with stipule-scars scarcely evident, glabrous; petioles stout, glabrous, $1\frac{1}{2}$ –2 cm. long, with a minute scutum or sometimes without any; leaves ovate, 12–22 cm. long, 7–14 cm. wide, shortly round-apiculate at the apex, rounded and submarginate-cordate at the base, *entire*, 7-nerved, infrequently pli-nerved, very prominently reticulate, *glabrous above and beneath*, coriaceous; panicles erect, moderate, pyramidal, many-flowered, about 10–12 cm. long; pedicels glabrous, 5–7 mm. long; hypanthium broadly cyathiform, glabrous, 8 mm. wide; calyx-limb truncate; petals obovate, retuse, 11–12 mm. long; filaments 6–8 mm. long; anther-sacs 10 mm. long; connectives ovoid, with a prominent dorsal and two prominent lateral lobes, acute or apiculate, 2–3 mm. long; style filiform, sharply bent over at the top, 10–18 mm. long.

COLOMBIA—*Lehmann* BT. 997 (Y, K).

This species is a densely branched tree, about 5 m. tall. The branches become slender and lightly arcuate. The leaves are widespreading, an intense shining green above and pallid beneath. The nerves are strong and deeply impressed above. The flowers have reddish petals. *A. Lehmannii* is perhaps most closely related to *A. grandifolia*, but the leaves are 7-nerved and entire, not 5-nerved and with margins sinuate-dentate.

15. *AXINAEA NITIDA* Cogn., Engl. Bot. Jahrb. 42: 138. 1906.

Branchlets obscurely tetragonal, furfuraceous-puberulent, becoming glabrous, *dark and conspicuously lustrous*; petioles slender, furfuraceous or glabrous, 1–4 cm. long, *with a tubercle-like scutum*; leaves narrowly ovate, 5–9 cm. long, $3\frac{1}{2}$ –5 cm. wide, short-acuminate at the apex, *rounded at the base*, undulate-denticulate, especially distally, sometimes nearly entire, 5-nerved, *with the reticulation elevated beneath*, glabrous and *lustrous* above, somewhat furfuraceous or glabrous beneath, coriaceous; panicles short, densely and many-flowered, about 6 cm. long; pedicels glabrous to slightly furfuraceous, 3–8 mm. long; hypanthium hemispheric, glabrous, 6–7 mm. wide; calyx-limb truncate to shallowly undulate; petals obovate, rounded to very slightly

retuse, 10–14 mm. long; filaments 6 mm. long; anther-sacs 5 mm. long; connectives ellipsoidal, blunt, 4 mm. long; style subfiliform, 11–15 mm. long.

PERU—Dept. of Amazonas, Molinipampa: *Weberbauer 4355*, type (B); *Mathews 1287* (K).

A. nitida is a shrub about 2 m. tall, with robust branches and dark lustrous branchlets. The flowers bloom in July, and have reddish petals. This species is similar to *A. grandifolia*. *A. nitida*, however, may be readily distinguished by its lustrous branchlets and upper leaf-surfaces, and its never decurrent leaf-bases.

16. *Axinaea robusta* D. Eves, sp. nov.

Ramuli robusti, manifeste tetragoni, ad nodos valde incrassati, cicatricibus stipularum manifeste incrassatis, furfuracei, demum glabri; petioli robusti, 2–4 cm. longi, furfuracei, scuto conspicuo; laminae ovato-lanceolatae, 9–16 cm. longae, 5–10 cm. latae, apice acuminatae, basi subrotundatae et parum auriculatae, auriculis nonnihil recurvis, valde minute sinuato-denticulatae vel subintegrae, 5–7-nerviae, supra glabratae, subtus praecipue ad venas venalaeque furfuraceae, subcoriaceae; paniculae pendulae, robuste pedunculatae, 15 vel plus cm. longae; pedicelli graciles furfuracei, 10 mm. longi; hypanthium semiglobosum, glabrum, 7 mm. latum; limbus calycis subtruncatus; petala suborbicularia, rotundata, 9 mm. longa; filamenta 4 mm. longa; thecae 6 mm. longae, connectivis ovoideis, planis, apiculatis, 4 mm. longis; stylus robustus, 7 mm. longus.

Branchlets robust, *conspicuously tetragonal, greatly swollen at the nodes, with stipule-scars prominently thickened*, furfuraceous, becoming glabrous; petioles robust, furfuraceous, 2–4 cm. long, with a conspicuous scutum; leaves ovate-lanceolate, 9–16 cm. long. 5–10 cm. wide, acuminate at the apex, *subrounded and small auriculate at the base*, with the auricles somewhat recurved, very minutely sinuate-denticulate or almost entire, 5–7-nerved, glabrous above, furfuraceous beneath especially along the nerves and veins, subcoriaceous; panicles pendulous, stoutly peduncled, 15 or more cm. long; pedicels slender, furfuraceous, 10 mm. long; hypanthium hemispheric, glabrous, 7 mm. wide; calyx-limb subtruncate; petals suborbicular, rounded, 9 mm. long; filaments 4 mm. long; anther-sacs 6 mm. long; connectives ovoid, flattened, apiculate, 4 mm. long; style stout, 8 mm. long.

COLOMBIA—Mont del Moro: *Purdie s.n.*, type (K).

Purdie records that he has observed panicles of this species 2–3 feet long. The small auriculate leaf-base is very significant, appearing much as if the auricles are expanded and somewhat recurved decurrent portions of the leaf blade. *A. robusta* is perhaps most closely related to *A. grandifolia*, differing from it principally by the conspicuously tetragonal branchlets greatly swollen at the nodes.

17. *AXINAEA COSTARICENSIS* Cogn., DC. Monogr. Phan. 7: 1182. 1891.

Branchlets obscurely tetragonal, scarcely swollen at the nodes, *with stipule-scars very prominent as thickened rings*, furfuraceous, becoming glabrous; petioles slender, glabrous to slightly furfuraceous, 2–4 cm. long, *with a tubercle-like scutum well below the blade and connected with it by narrow lateral recurved wings*; leaves ovate, 9–18 cm. long, 5–8 cm. wide, obtuse at the apex, narrowed and subrounded at the base, entire or minutely and remotely denticulate, 5–7-nerved, glabrous above, glabrous to slightly furfuraceous beneath, submembranaceous; panicles erect or subpendulous, broadly pyramidal, many-flowered, about 20 cm. long; pedicels furfuraceous, 5–10 mm. long; hypanthium hemispheric, essentially glabrous, 7 mm. wide; calyx-limb subtruncate; petals obovate, retuse, 10–15 mm. long; filaments 3 mm. long; anther-sacs 3 mm. long; connectives ovoid, apiculate in the rear, 3 mm. long; style 5–10 mm. long.

COSTA RICA—Isla del Rio Mancaron: *Pittier 2007*, type (B), isotype (F); Varablanca, Sarapiquí: *Werckle 16687* (F).

A. costaricensis occurs at an altitude of about 2100 m. It is the only species of *Axinaea* that has as yet been found outside of South America. This species is probably most nearly related to *A. grandifolia*.

18. *AXINAEA GRANDIFOLIA* (Naud.) Triana, Trans. Linn. Soc. Bot. 28: 69. 1871.

Chastenea grandifolia Naud., Ann. Sci. Nat. III. 18: 122. 1852.

Branchlets obtusely tetragonal, pulverulent near the tips, becoming glabrous; petioles slender, pulverulent, 3–4 cm. long, *with a transverse tubercled scutum*; leaves narrowly ovate, 7–16 cm. long, 6–7 cm. wide, shortly round-apiculate at the apex, rounded and *generally shortly decurrent* at the base, in the latter case the lower extremity of the decurrent portion recurved or expanded and crisped, sinuate-dentate, 5–7-nerved, more or less conspicuously reticulate, glabrous above, glabrous to somewhat furfuraceous beneath, coriaceous; panicles erect, many-flowered, subcorymbose; pedicels pulverulent, 8–12 mm. long; hypanthium broadly hemispheric, glabrous or essentially so, 7–8 mm. wide; calyx-limb subentire; petals broadly obovate, retuse to apiculate, 10–12 mm. long; filaments 2 mm. long; anther-sacs flattened, 5 mm. long; connectives ovoid to rotund, apiculate to blunt, 2 mm. long; style robust to subfiliform, slightly arcuate, 7–8 mm. long.

VENEZUELA—Prov. of Merida: *Moritz 959*, cited by Cogn. (B, K), *Funck and Schlim 1253*, cited by Cogn. (G). COLOMBIA—Dept of Santander: *Kalbreyer 749* (B, K). PERU—Huanuco, Pan de Azucar: *Sawada 68* (F).

A. grandifolia has purple-petaled flowers. This species is somewhat variable. It is probably most closely related to *A. macrophylla*, which it

more or less resembles. *A. grandifolia*, however, has a petiolar-scutum and flowers distinctly smaller and more numerous.

19. *AXINAEA MACROPHYLLA* (Naud.) Triana, Trans. Linn. Soc. Bot. 28: 69. 1871.

Chastenea macrophylla Naud., Ann. Sci. Nat. III. 18: 121. 1852.

Chastenea floribunda Naud., Ann. Sci. Nat. III. 18: 122. 1852.

Axinaea floribunda (Naud.) Triana, Trans. Linn. Soc. Bot. 28: 69. 1871.

Branchlets obscurely tetragonal, glabrous to densely brown-pulverulent; petioles slender, glabrous or furfuraceous, 2-4 cm. long, *without a scutum*; leaves elliptical, 7-12 cm. long, 2-5 cm. wide, acute or shortly round-apiculate at the apex, *rounded or somewhat attenuate with recurved margins at the base*, sinuate-serrate at least distally or almost entire, *7-nerved*, glabrous above, glabrous or furfuraceous beneath, coriaceous; panicles pendulous, compact, cymose, short; pedicels furfuraceous, 5-10 mm. long; hypanthium hemispheric, glabrous or scarcely furfuraceous, 6-8 mm. wide; calyx-limb truncate or distinctly 5-sinuate; petals obovate, retuse, 8-12 mm. long; filaments 4-6 mm. long; anther-sacs 5-7 mm. long; connectives broad, flattened, obtuse or acute, 3-5 mm. long; style 8-15 mm. long.

COLOMBIA—Bogota: *Woronow & Juzupczuk* 5084 (Y), *Triana s.n.* (Y, K), *Holton* 907 (Y, K), *Tracey* 299 (K); Dept. of El Cauca: *Pennell & Killip* 6506 (Y, B), *Pennell* 7112 (Y), *Killip* 6798 (Y); Quindio: *Triana s.n.* (Y); *Bro. Ariste-Joseph B-14* (Y); *Triana* 5832 (Y, K); *Jameson* 451 (K, G); Central Andes of Popayan: *Blakes* 8649 (K); Eastern Paramos of Guasca: *Bro. Ariste-Joseph s.n.* (F); Antioquia: *Lehmann* 7446 (B), *Pennell* 4259 (Y); Dept. of Santander: *Killip & Smith* 17824 (Y, F), *Killip & Smith* 17834 (Y); Dept. of Caldas: *Killip & Hazen* 9474 (Y); *Linden* 768 (F, K); *Lehmann* 8649 (Y). ECUADOR—Prov. of Azuay and Canar, between Cuenca and Huigra: *Hitchcock* 21677 (Y); Prov. of Loja: *Hitchcock* 21436 (Y); *Spruce* 5831 (K, B); *Lehmann* 4653 (B); *White* 4772 (K).

A. macrophylla is a shrub or tree occurring at an altitude of 1800-3300 m. The petals are pale-pink to deep-pink, sometimes white. The flowers blossom in October and November. This species is perhaps most closely related to *A. grandifolia*, from which it differs principally in the absence of a petiolar-scutum. *A. macrophylla* bears some resemblance to *A. affinis*. In the former, however, the submarginal nerves are the 6th and 7th, whereas in the latter they are the 4th and 5th.

Formerly, *A. macrophylla* and *A. floribunda* were considered as separate species. Comparison of a large number of herbarium specimens, however, shows that the one grades imperceptibly into the other. Accordingly, I have here combined the two groups into the one species: *A. macrophylla*.

The "Index Kewensis" lists *Chastenea affinis* Naud. as a synonym for *A. macrophylla*. Cogniaux, however, (DC. Monogr. Phan. 7: 1891) records *C. affinis* as a synonym for *Axinaea affinis* Cogn. In the present paper Cogniaux's synonymy is looked upon as the correct one and is, accordingly, herein adopted.

20. AXINAEA AFFINIS (Naud.) Cogn., DC. Monogr. Phan. 7: 449. 1891.

Chastenea affinis Naud., Ann. Sci. Nat. III. 18: 120. 1852.

Axinaea macrophylla (Naud.) Triana, pro parte, Trans. Linn. Soc. Bot. 28: 69. 1871.

Branchlets obscurely tetragonal, glabrous; petioles slender, glabrous, 1–2 cm. long, without a scutum; leaves ovate, 4–5 cm. long, 2–3 cm. wide, obtuse at the apex, acute and shortly revolute-decurrent at the base, remotely sinuate-serrate, especially so distally, 5-nerved, with the secondaries conspicuous and brown, prominently reticulate, glabrous above, very thinly furfuraceous beneath or glabrous, coriaceous; panicles pendulous, cymose, few flowered; pedicels essentially glabrous, 10 mm. long; hypanthium hemispheric, essentially glabrous, 7 mm. wide; calyx-limb truncate; petals obovate, retuse, 12–15 mm. long; filaments 6–8 mm. long; anther-sacs 6 mm. long; connectives ovoid, with a prominent dorsal lobe, acuminate; style thickish, 15–20 mm. long.

COLOMBIA—Prov. of Ocaña: *Schlim* 304, cited by Cogn. (K). ECUADOR—between Sarajuro and San Lucas: *Jameson* 143 (K); San Lucas: *Jameson s.n.* (F).

A. affinis occurs at an altitude of 3300–3700 m. The leaves are intensely green above and pale beneath. The petals are purple. This species is somewhat similar to *A. Merianiae* and *A. macrophylla*. It differs, however, from the first in having leaves not at all pli-nerved and a hemispheric hypanthium, and from the second in having leaves 4–5 cm. long with the submarginal nerves the 4th and 5th. *A. affinis* is probably most closely related to *A. macrophylla*. The synonymy listed above is taken from Cogniaux (DC. Monogr. Phan. 7: 449. 1891).

21. AXINAEA MERIANIAE (DC.) Triana, Trans. Linn. Soc. Bot. 28: 69. 1871.

Chastenea Merianiae DC. Prodr. III. 102. 1828.

Branchlets obscurely tetragonal, becoming terete, glabrous; petioles slender, glabrous, 1½–2 cm. long, without a scutum; leaves elliptical, 4–6 cm. long, 2½–3 cm. wide, acute or obtuse at the apex, acute to narrowed and shortly revolute-decurrent at the base, with the decurrent portion sometimes conspicuously expanded and reflexed, sinuate-serrate, 3–5-ply-nerved, glabrous above and beneath, subcoriaceous; panicles subnuttant, somewhat corymbose,

few-flowered, short; pedicels glabrous, 10 mm. long; *hypanthium* shallowly saucer-shaped or broadly campanulate and depressed, glabrous, 7–10 mm. wide; calyx-limb dilated, often reflexed, truncate to shallowly 5-sinuate; petals obovate, retuse, 12–15 mm. long; filaments 3–5 mm. long; anther-sacs 4 mm. long; connectives ovoid to rotund, large, blunt, 3–4 mm. long; style attenuate, 9–15 mm. long.

ECUADOR—Tambo de Cotosacapi: Seemann 770, cited by Cogn. (K); Azogues: Lehmann 8533 (B). PERU—Dept. of Piura, prov. of Ayavaca: Weberbauer 6371 (F, Y, B); Dept. of Libertad, prov. of Otuzco: Weberbauer 6997 (B).

A. Merianiae is a shrub up to 5 m. tall, occurring at an altitude of 2900 m. The flower has a white to rose-colored corolla, and stamens with white filaments, yellow anthers, and dark red-violet connectives. This species is probably most closely related to *A. affinis*, which it often somewhat resembles. *A. Merianiae*, however, has leaves 3–5-ply-nerved, a depressed hypanthium, and large more or less ellipsoidal connectives which are blunt in the rear. *A. affinis*, on the other hand, has 5-nerved leaves (not at all pli-nerved), a broadly hemispheric hypanthium, and ovoid connectives which are acuminate in the rear.

22. AXINAEA LEPIDOTA (Benth.) Triana, Trans. Linn. Soc. Bot. 28: 69. 1871.

Chastenea lepidota Benth., Pl. Hartw. 182. 1845.

Chastenea coriacea Naud., Ann. Sci. Nat. III. 4: 55. 1845.

Branchlets more or less tetragonal, whitish-arachnoid on the younger parts; petioles slender, whitish-arachnoid when young, 8–12 mm. long, without a scutum; leaves elliptical, 3–5 cm. long, 1–2 cm. wide, obtuse at the apex, rounded and sometimes slightly revolute-decurrent at the base, entire or minutely and remotely sinuate on the upper half, 3–5-ply-nerved, sometimes only scarcely pli-nerved, glabrous above, whitish-arachnoid beneath especially when young, coriaceous; panicles erect, cymose, few-flowered, short; pedicels whitish-arachnoid to scarcely so, 5–10 mm. long; hypanthium hemispheric, glabrous or scarcely whitish-arachnoid at the base, 10–11 mm. wide; calyx-limb subtruncate; petals obovate, strongly asymmetrical, apiculate, 14 mm. long; stamens often stunted or imperfectly developed; filaments 7–8 mm. long; anther-sacs attenuate, normally 9 or more mm. long; connectives ovoid, acute or apiculate, 2 mm. long; style sometimes slightly arcuate, 10–12 mm. long.

ECUADOR—Province of Cuenca: Hartweg 1014, type (K), isotypes (B, G), Lehmann 4924 (F, B), Jameson 15 (K); Prov. of Loja: Rose 23116 (Y), Hitchcock 21573 (Y); Tipococha: Diels 546 (B); Nabon: Rose 22992 (Y); Jameson s.n. (F).

A. lepidota is a shrub up to 2-3 m. tall, occurring at an altitude of 2900-3300 m. The leaves are shining green above, becoming nigrescent when dry. This species is characterized, at least when young, by a whitish arachnoid pubescence. It is probably most closely related to *A. affinis* or *A. Merianiae*. It differs from these, however, in having smaller leaves (commonly less than 5 cm. long) and the whitish-arachnoid pubescence.

DOUBTFUL SPECIES

Axinaea quitensis R. Benoist, Bull. Soc. Bot. France 81: 326. 1934.

Because the type is not available and because the description is not distinctive enough, I am unable to definitely consider this species. It is not possible, I believe, from the description of the species to distinguish between it and *A. macrophylla* Triana. Benoist asserts that *A. quitensis* differs from *A. macrophylla* by its glabrous condition, its clearly lobed calyx-limb, and its much smaller leaves (6-8 cm. long). Upon an examination of a large number of *A. macrophylla* specimens, however, these distinctions do not, in my opinion, appear to hold.

ECUADOR—Paramo de San Juan: *Benoist 3941*, type (Paris), not available.

EXCLUDED SPECIES

Axinaea tetragona Cogn., Engl. Bot. Jahrb. 42: 137. 1908.

This species is excluded because it does not have the characteristic *Axinaea* stamen. The connectives are scarcely inflated and have two spurs, one projecting from the rear and another ascending parallel to the anthersacs. The structure is that of *Meriania*. The species appears to be most closely related to *M. radula* Triana, differing mainly in having the leaves smooth above instead of rough. I have not, however, examined any specimens of *M. radula* for comparison.

PERU—Dept. of Amazonas, between Tambo Almirante and Tambo Bagazan: *Weberbauer 4430* (B), labeled as the type specimen of *Axinaea tetragona* Cogn.

NEW YORK BOTANICAL GARDEN,
NEW YORK CITY, N. Y.

INDEX TO AMERICAN BOTANICAL LITERATURE

1931-1935

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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New Rhodophyceae from Woods Hole¹

CHIN-CHIH JAO

(WITH PLATES 10-13)

During the summers of 1933 and 1934, as the writer worked on both freshwater and marine algae of New England at the Marine Biological Laboratory, Woods Hole, Massachusetts, a number of new species were discovered. The freshwater forms have been reported under three titles in *Rhodora* and the *Transactions of the American Microscopical Society*. It is now proposed in this initial report to deal with species and records new to North America of the marine genera *Acrochaetium*, *Colaconema*, *Cruoriopsis* and *Erythropeltis*. These plants are all small forms, either epiphytic, endophytic, endozoic or epizoic. The members of *Acrochaetium* are most abundant between the tide marks or just below low tide on other red, brown or green algae, excepting *A. Alcyonidiae* and its variety *cylindricum* which were found on *Alcyonidium Mytili* washed on shore from rather deep water. The remaining genera were all deep water forms.

This study was made under the direction of Professor Wm. R. Taylor, University of Michigan, to whom the author is deeply grateful for his help and advice.

ERYTHROPELTIS DISCIGERA Schmitz var. FLUSTRAE Batters

(Pl. 13, figs. 1, 2)

Fronds rose-colored, parenchymatous, of one cell layer, horizontally extended on the surface of the host, orbiculate, with irregular margin, up to 192μ in diameter; cells polygonal, oblong or irregular, irregularly arranged, $5-10 (-13)\mu$ by $3-7 (-10)\mu$; chromatophore single in each cell, parietal; gonidia globose, from 6 to 7μ in diameter, each being isolated from the vegetative cell by an oblique and curved wall.

This genus and species is new to North America. It is quite similar to the typical form as described by Batters, except that the gonidium is a little smaller. These plants were found on *Alcyonidium Mytili* Dalyell, washed on shore, Sheep Pen Harbor, Nonamesset Island, Woods Hole, Massachusetts, Sept. 1, 1934.

Colaconema americana, sp. nov.

(Pl. 13, fig. 8)

Filamentis endophyticis, valde et irregulariter ramosis, fluenter innexibus inter cellulas corticales plantae matricis efficientibus; ramis lateralibus sparsis

¹ Papers from the Department of Botany and Herbarium of the University of Michigan, No. 548.

vel oppositis, sub angulo recto plerumque egredientibus, cellulis formo variis, plerumque in media valde tumidis, 5-10, interdum ad 32μ altis, 16-55, plerumque 22- 38μ longis, membrana transversa $3-5\mu$ altis; filamentis erectis extra corticali hospitis a filamentis endophyticis ramosis, multis et tenuis, longitudine 2-4- plerumque 3-cellularibus, apicem versus paulo attenuatis, cellulis forma cylindricis, cellulis basalis chromatophoro tenuiter evoluta, $3-5\mu$ altis, 13- 32μ longis, cellulis terminalibus hyalinis, solum 2.5- 3.0μ altis; chromatophoris singulis, leviter lobatis, parietalibus, roseo-rubribus; monosporangiis sessilibus, frequenter in ramulis terminalibus lateralibus confertis, subglobosis, 9.6- 13.0μ altis, vel in axis aut ramulis principalibus lateralibus solitariisque, forma depresso-globosis, subglobosis, lenticularibus vel hemisphaericis, 9.5- 13.0μ latis, 6- 13μ longis, raro in ramulis abbreviatis terminalibus; parte cellulae haud in monosporam mutata quasi operculum sporangii efficiente, crassitudine variabili, eiusdem genere vel leviter lamellose.

Endophytic filaments much and irregularly branched, interweaving between the cortical cells of the host plant; side branches arising from the main filaments or branches mostly nearly at right angles, scattered or opposite, cells varying in form, generally greatly tumid at intervals, 5-10 sometimes swollen up to 32μ diameter, 16-55, mostly 22- 38μ long, cross walls $3-5\mu$ diameter; from the endophytic filaments are produced the numerous, slender, and erect filaments free from the cortical layer of the host, 2 to 3, mostly 3 cells in length, their cells cylindrical in form, tapering toward the end, basal cells containing very poorly developed chromatophores, $3-5\mu$ diameter and 13- 32μ long, terminal cells colorless, only 2.5- 3.0μ in diameter; chromatophore single in each cell, slightly lobed, parietal, rose-colored; monosporangia sessile, globose, often clustered on the short lateral branches, 9.6- 13.0μ diameter, or solitary and lateral on the main filaments or branches, depressed-globose, subglobose, lenticular or hemispherical in form and 9.5- 13.0μ diameter, 6- 13μ long, rarely solitary and terminal on the short branches; monospore formed from part of the cell contents of the monosporangium, the remaining part forming a cup-like base below the monospore varying in thickness, and homogeneous or slightly lamellose.

The cup-like bases of the monosporangia are one of the quite remarkable characteristics of this genus. All the known species of this genus have the fronds entirely endophytic. This new species is separated from them by the presence of the distinct, numerous, short, erect and free hairlike filaments. Furthermore, it differs from *Colaconema Bonnemaisioniae* Batters in having larger vegetative cells and interwoven filaments, from *C. Asparagopsidis* Chemin in having the monosporangia otherwise than strictly solitary and terminal on the branches, and the vegetative cells greatly tumid, from *C. Chylocladiae* Batters in not having the filaments united by lateral branches, by the vegetative cells being generally greatly swollen, and greater dimensions, and from *C. reticulatum* Batters, an in-

completely known species, in not having the fronds anastomosing, in never having side branches appressed to the main filaments or branches to form one filament with a double row of cells, and in having the length of the vegetative cells generally greater than the diameter.

This genus is one of the new records for North America. These new plants were found very abundantly in *Asparagopsis hamifera* (Hariot) Okamura from Gay Head, Marthas Vineyard, Massachusetts, July 17, 1934. Type in C.-C. Jao collections and Herb. Univ. Mich., *Woods Hole No. 272*.

***Acrochaetium unifilum*, sp. nov.**

(Pl. 10, figs. 26-32)

Thallo minutissimo, epiphytico; cellula basali singula subhemisphaerica, filamenta erecta plerumque non ramosa, solitaria, rarissime bina, 1- 9-cellula, a facie laterali cellulae basalis emergente, plus minusve curvata, plerumque ad hospitis superficiem parallela; cellulis vegetativis plus minusve tumidis, 6.5-13 μ latis, 13-16 μ longis; pilis plerumque pseudolateralibus, interdum terminalibus; chromatophoro stellari pyrenoideo centrali instructo; monosporangiis sessilibus, rarissime pediculo unicellulo, unilateribus, interdum 2 in cellulis singulis, ovatis, frequenter minoribus quam cellulis vegetativis, 5-6.4 μ latis, 8-9.6 μ longis; monosporiis liberis globosis, circa 7 μ latis; articulo primo fili erecti exhibitum lateraliter a monospora germinate.

Plants very small, epiphytic, attached to the host by a single subhemispherical basal cell, giving rise to a single unbranched, 1- to 9-celled and erect filament from the lateral face, very rarely a second 1- to 3-celled short filament also arises from the same basal cell; filaments more or less arched, generally parallel to the surface of the host, about the same diameter throughout the whole plant; vegetative cells more or less tumid in the middle, 6.5-13 μ diameter, 13-16 μ long; hairs usually pseudolateral, sometimes terminal; chromatophore stellate, usually with four rays, with a central pyrenoid; monosporangia sessile, very rarely with a 1-celled pedicel, unilateral, sometimes two on each cell, oval in form, usually smaller than the vegetative cells, 5-6.4 μ diameter, 8-9.6 μ long; free monospores globose, about 7 μ in diameter; when the monospore attaches to the host, it is gradually flattened on its attaching side and becomes hemispherical; the first articulation of the erect filament is laterally produced from the monospore and results in a single filament parallel to the host plant; sexual reproduction unknown.

These new plants are probably near to *Acrochaetium microscopicum* Naeg., but differ from it in having an unbranched erect filament arising from the basal cell laterally, the vegetative cells not bead-shaped, the hairs mostly pseudolateral and rarely terminal, and the monosporangia mostly only half the diameter of the vegetative cells.

Epiphytic on *Arthrocladia villosa* Duby, Norton Point, Marthas Vineyard, Massachusetts, Aug. 3, 1934. Type in C.-C. Jao collections and Herb. Univ. Mich., *Woods Hole No. 274*.

***Acrochaetium microfilum*, sp. nov.**

(Pl. 10, figs. 1-5)

Fronde minutissima, epiphytica, 40-60 μ alta, 20-35 μ longa (pilis exceptis); cellula basali solitaria globosa, maiore quam filamentae cellulis, circa 6.5 μ diametro; fila plerumque 3, interdum 4, plana una sola et recta 2- vel 6-cellulares gignente; filis exterioribus plus extentis, directis vel paulo recurvatis, in hospite ferme decumbentibus; ramulis lateralibus vel dichotomis, cellulis doliiformibus, 3-5 (-6) μ latis, 3-5 (-6) μ longis; cellula terminali apicem versus sensim in pilum hyalinum attenuati; chromatophoro parietali, cellulam complenti vel paene complenti, pyrenoideo centrali instructo; monosporangiis regulariter secundis in filis aequis et secundis vel sparsis in filis erectis, plerumque sessilibus, rarius pediculo unicellulo, forma ovatis, 3-5 μ altis, 6.5-8.0 μ longis.

Plants epiphytic, very small, 40-60 μ wide, 20-35 μ tall; basal cell single and globose, larger than the filament cells, about 6.5 μ in diameter, with rather thick wall, from which are produced often three, sometimes four, free main filaments in a single vertical plane, 2-6 cells long, the outside two filaments more extended, straight or slightly arched downward, almost decumbent on the host, the remaining filament or filaments erect, branches lateral or dichotomous, cells barrel-shaped, 3-5 (-6) μ diameter, 3-5(-6) μ long; the terminal cell tapering toward the end to form a hyaline hair; chromatophore parietal, filling or nearly filling the cell, with a central pyrenoid; monosporangia regularly secund on the horizontal filaments, secund or scattered on the erect filaments, mostly sessile, rarely with one-celled stalks, oval in form, 3-5 μ diameter, 6.5-8.0 μ long.

This species should be compared with *Acrochaetium crassipes* Børgesen, *A. trifilum* Batters, *A. parvulum* (Kylin) Hoyt and *A. pulchellum* Børgesen, but it differs from the first in having the chromatophores not stellate, and a globose basal cell; from the second in not having the monosporangia globose; from the third in never having the monosporangia opposite in arrangement; from the fourth in having the basal cell undivided, the filament not creeping on the host, but in a regular fan-shaped arrangement; and from all of them in having smaller dimensions of all cells.

Found on *Polysiphonia fibrillosa* together with several other species of *Acrochaetium*, Norton Point, Marthas Vineyard, Massachusetts, Aug. 3, 1934. Type in C.-C. Jao collections and Herb. Univ. Mich., *Woods Hole No. 274*.

***Acrochaetium compactum*, sp. nov.**

(Pl. 10, figs. 6-14)

Thallo epiphytico, minutissimo, 22-42 μ longo et 38-61 μ alto (pilis exceptis); cellula basali singula globosa vel subglobosa, membrana crassa, plerumque grandiore quam filamentarum cellulis, circiter 8-10 μ alta; filis erectis plerumque 3, interdum 2 vel 4, a cellula basali ramosis, valde expandis, plus minusve irregulariter ramosis, ramulis brevibus plantarum nitidarum frequenter fascicularibus, apicem versus sensim paulum attenuatis, cellulis doliiformibus, 5-8 μ altis, 5-10 μ longis; pilis terminalibus; chromatophoro stellaeformi, pyrenoido centrali instructo; monosporangiis sessilibus, terminalibus, secundis vel sparsis, raro oppositis, 1 vel 2 in articulis singulis, ovatis vel subglobosis, 5.0-6.5 μ altis, 6.5-7.0 μ longis.

Plants epiphytic, very small, 22-42 μ tall and 38-61 μ broad (except hairs); basal cell single, globose or subglobose, with a thick wall, especially on the lower side, generally larger than the filament cells, 8-10 μ diameter, from which are produced mostly three, sometimes two or four erect main filaments more expanded in a single plane, more or less irregularly branched, branchlets of the well developed plants frequently tufted, gradually slightly tapering toward the end, cells barrel-shaped, 5-8 μ diameter, 5-10 μ long; hairs terminal; chromatophore stellate, with a central pyrenoid; monosporangia sessile, terminal, second or scattered, rarely opposite, mostly 1, sometimes 2, on each articulation, ovate or subglobose, 5.0-6.5 μ diameter and 6.5-7.0 μ long.

These plants are related to *Acrochaetium moniliforme* (Rosenvinge) Børghesen and *A. crassipes* Børghesen, but differ from the first in having lesser dimensions of all cells and the branchlets tufted in well developed plants, and from the second in having the filaments often more than two, the basal cell globose in form, and the branchlets tufted.

Very abundant on *Cladophora* sp. from Black Rock, Sconticut Neck near Fairhaven, New Bedford, July 25, 1934. Type in C.-C. Jao collections and Herb. Univ. Mich., *Woods Hole* No. 275.

***Acrochaetium moniliforme* (Rosenvinge) Børghesen**var. ***Mesogloiae*, var. nov.**

(Pl. 10, figs. 15-17)

Thallo minuto, epiphytico, 40-90 μ alto et 40-65 μ longo (pilis exceptis); cellula basali singula subglobosa vel subovata, 8.0-9.6 μ lata, 11-17 μ longa, membrana basali crassitudine usque ad 3.5-5.0 μ et plus minusve distincte lamellosa, forma subhemisphaerica, intra membranum gelatinosum immerse et cellulum circumdatum hospitis adjuncto; fila plerumque 1, rarissime 2 vel 3, plus minusve recurvata; thallo unifilamentio plerumque 1 vel 2 ramulis ex cellula prima filii, plus minusve dichotomis vel interdum oppositis, apicem versus sensim paulum attenuatis, cellulis apiceis 6.5 μ latis, 9.6 μ (pilis exceptis)

longis, cellulis reliquis $8.0-9.5\mu$ latis, $6.5-9.6\mu$ longis, doliiformibus, membrana tenui; pilis terminalibus, stabilibus, 1 vel 2 in omnis cellulis terminalibus; chromatophoro stellaeformi, pyrenoideo centrali instructo; monosporangiis ovatis, $6.5-8.0\mu$ latis, $9.5-16.0\mu$ longis, plerumque sessilibus, interdum pediculo unicellulo, saepe in articularum singulorum parte superiore secundis, raro oppositis.

Plants minute, epiphytic, $40-90\mu$ wide, $40-65\mu$ tall; basal cell subglobose to subobovoid, $8.0-9.6\mu$ diameter; $11-17\mu$ long, with a subhemispherical basal wall up to $3.5-5.0\mu$ thick, more or less distinctly lamellose, immersed in the mucilage layer and attached to the peripheral cells of the host; from the basal cell producing mostly 1, very rarely 2-3 main filaments, more or less recurved; in the single filament type, generally one or two strong branches arise from the first cell of the main filament, branches few, as thick as the main filament, more or less dichotomous in form, or sometimes opposite, gradually a little tapering toward the end, tip cells about 6.5μ diameter and 9.6μ long (except hairs), the other cells $8.0-9.5\mu$ diameter, $6.5-9.5\mu$ long, barrel-shaped, cell wall thin; hairs present in all stages, thick, basal parts $3.0-3.5\mu$ diameter, up to 120μ long, one or two terminal on the tip cell; chromatophore stellate, with a central pyrenoid; monosporangia oval, $6.5-8.0\mu$ diameter, $9.5-16\mu$ long, mostly sessile, occasionally with a 1-celled stalk, often secund on the upper side of each articulation, rarely opposite.

This variety differs from the typical species in having the main filament usually single, the main branches arising from the cell adjoining the basal cell, which is greatly thickened on the lower side; the thick hairs occurred in all stages, and the ramification was mostly dichotomous.

Plants found on *Mesogloia divaricata* (Ag.) Kütz., Sheep Pen Harbor, Nonamesset Island, in the Elizabeth Island chain off Woods Hole, Massachusetts. Type in C.-C. Jao collection and Herb. Univ. Mich., *Woods Hole No. 276*.

***Acrochaetium intermedium*, sp. nov.**

(Pl. 11, figs. 1-4)

Thallo endophytico, 1-2 mm. alto, cellulis basalibus elongatis, $13-16\mu$ altis, $32-57\mu$ longis, 1-3 filis rhizoideis gignentibus, longitudine 1- vel 5-cellularibus; parte inferiore cellulae basalis et filis rhizoideis in vel inter membranum hospitis penetratis; filamentis erectis singulis, a basi ramosis, ramulis secundariis regulariter secundis, cellulis $8-10\mu$ altis, (26-) $32-64\mu$ longis; cellula terminali leviter attenuati, crassitudine circa 6.5μ ; chromatophoro parietali pyrenoideo centrali instructo; sine pilis; bisporangiis et monosporangiis cylindrico-obovoideis vel ovatis, $9-13\mu$ altis, $19-23\mu$ longis, plerumque sessilibus, rarius pediculo unicellulo, in cellulis ramulorum inferioribus secundis, 2-6-seriatis, interdum unilateraliter sparsis in parte superiore filorum principium, cellula inferiore plerumque longiore quam superiore.

Plants endophytic, 1–2 mm. tall; the base consisting of the original spore, which elongates downward to form a cuneate prolongation, penetrating into the host plant between or in the cell walls, from the basal cell, or rarely from the adjoining cell, giving rise to one to three rhizoidial filaments of 1–5 cells in length, wholly imbedded in cell walls of the host plant, except those rhizoids which rise from the adjoining cell, the upper part of the basal cell retaining the original spore form, 13–16 μ in diameter, but elongated to 32–57 μ ; from each spore a single erect main filament arises, ramifying by numerous long branches beginning near the basal cell; secondary branches regularly secund, cells 8–10 μ diameter, (26–) 32–64 μ long, terminal cells tapering, with a diameter about 6.5 μ ; chromatophore parietal, a little lobed on both ends, generally occupying the upper end of the cell, with a prominent central pyrenoid; hairs absent; bisporangia and monosporangia cylindric-ovate to ovate, 9–13 μ diameter, 19–23 μ long, secund, mostly sessile, rarely 1-celled pedicellate, placed upon the lowermost cells of the branches or branchlets, two to six on each branch, occasionally also scattered unilaterally on the upper part of the main filaments; the upper cell of the bisporangium is generally shorter than the lower.

The writer's materials are rather past their full maturity. The upper cells of the bisporangia are mostly empty and only a few bisporangia were found containing spores in both upper and lower cells. The empty bisporangia were commonly divided by a very clear, straight cross wall, especially when placed upon the lowest articulations of the branches.

These plants have some characteristics of both *Acrochaetium Dasyae* Collins and *A. opetigerum* Børjesen, but differ from the first in having an endophytic base, an elongated basal cell (original spore) often with rhizoidial filaments penetrating into the cell wall of the host, greater dimensions of all cells, and much more abundant branching; from the second in having the secondary branches regularly secund; and from both in having the sporangia quite often divided into two cells.

The plants are abundant and mostly grow at the fork of the pinnules of the host plants, *Dasya pedicellata* C. Ag., rarely on other parts. Collected from Grassy and Pine Islands, Woods Hole, Massachusetts, Aug. 7, 1934. Type in C.-C. Jao collections and Herb. Univ. Mich., *Woods Hole No. 277*.

***Acrochaetium subseriatum*, sp. nov.**

(Pl. 11, figs. 5–7)

Thallo epiphytico, cellula basali elongata, membrana crassa, filis repentibus depravatis e cellula basali et cellula adjacentia ramosis; filum erectum a spora mutabili orientem, altitudine usque ad 2–3 mm., a basi magna parte ramosis, ramis inferioribus valde longioribus quam superioribus; ramis secundariis crebris, secundis vel alternis; cellulis 6.4–9.6 μ altis, 32–70 μ longis;

pilis terminalibus, rarissimis; chromatophoro parietali pyrenoideo centrali instructo; monosporangiis sessilibus vel pediculo unicellulo, secundis prope basim ramorum, raro sparsis, cylindrico-ovatis, $6.5-9.5\mu$ altis, $22-31\mu$ longis.

Plants epiphytic; basal cell elongate, with a thick wall, with the adjoining cell giving rise to contorted creeping filaments; solitary erect main filament arising from the modified spore cell, up to 2-3 mm. tall, freely branched, the lowest branches quite near the base, much longer than the upper ones, gradually shorter upward, branchlets very numerous, secund or alternate, cells $6.4-9.6\mu$ diameter, $32-70\mu$ long; hairs terminal, very rare; chromatophore parietal, containing a central pyrenoid; monosporangia mostly borne on each articulation of the branchlets, sessile or with 1-celled stalks, secund near the base of the branchlets, rarely scattered, cylindric-obovoid in form, $6.5-9.5\mu$ diameter, $22-31\mu$ long.

These plants are related to *Acrochaetium seriatum* Børgesen and *A. Sagraeanum* (Mont.) Bornet, but differentiated from both in that erect filaments do not arise from the creeping filaments, and the cylindric-obovoid monosporangia are much longer. The basal part of *A. seriatum* Børgesen consists of short, irregularly bent, creeping filaments, fusing together in the middle into a small disc. In *A. Sagraeanum* (Mont.) Bornet the basal layer is composed of contorted and entangled filaments, from which the erect filaments arise.

Plants epiphytic on *Zostera*, mixed with *Acrochaetium virgatulum* var. *luxurians*. Collected from Nobska Point, Woods Hole, Massachusetts, Aug. 25, 1933. Type in C.-C. Jao collections and Herb. Univ. Mich., *Woods Hole No. 278*.

ACROCHAETIUM ATTENUATUM (Rosenvinge) Hamel 1927

(Pl. 12, fig. 1)

Plants epiphytic; basal filaments fused together near the center to form a 1-layered disc, ramification mostly dichotomous or opposite, irregularly extended from the center, cells $6.5-9.5\mu$ diameter, $6.5-11\mu$ long; erect filaments numerous, arising from the central part of the basal disc, up to 250 (or more) μ tall, ramification scattered, opposite or dichotomous, the terminal cells tapering toward the tip and forming a terminal hyaline hair, cells $5.0-6.5\mu$ diameter, $(6.5-9.5-16\mu)$ long; chromatophore parietal, with a prominent pyrenoid; monosporangia occur mostly on the upper part of the plant and usually are solitary, mostly sessile, sometimes with a 1-celled stalk, oval in form, $4.0-6.5\mu$ diameter, $6.5-9.6\mu$ long.

These plants as described above seem to be very close to *Acrochaetium attenuatum* (Rosenvinge) Hamel, except that the erect filaments are shorter and hairs do not disappear on the longest filaments. Probably the writer's samples are in a rather young condition, but the growth habit and measure-

ments are quite in accord. This species is newly recorded for North America.

Found on *Polysiphonia fibrillosa* together with several other species of *Acrochaetium*, Norton Point, Marthas Vineyard, Massachusetts, Aug. 3, 1934.

Acrochaetium Alcyonidiae, sp. nov.

(Pl. 12, figs. 2-4)

Filamentis basalibus endozoicis, valde longioribus quam filamentis erectis, intra hospitem penetratis, raro partibus epizoicis, abunde at plerumque dichotomiter ramosis, cellulis plerumque medio tumidis, $6.5-13\mu$ latis, $13-32\mu$ longis; filamentis erectis usque ad 600μ altis; ramulis plerumque 1-5-, interdum ad 10-, cellularibus, brevissimis, secundis vel sparsis, cellulis $6.5-9.5\mu$ latis, $9.5-19\mu$ longis; sine pilis; chromatophoro parietali, pyrenoideo centrali instructo; monosporangiis obovoideis, sessilibus vel pediculo unicellulo, 1 vel 2 in ramulorum articulissingulis, terminalibus vel secundis, plerumque dense confertis, $8.0-9.5\mu$ latis, (13-) $16-19\mu$ longis, interdum bisporangiis repositis.

Plants endozoic below, the basal filaments much longer than the erect filaments, deeply penetrating into the host between the individuals of the colony, rarely a part of them epizoic, abundantly and usually dichotomously branched, the cells varying in size and shape, $6.5-13\mu$ diameter, $13-32\mu$ long, often swollen in the middle; the free filaments erect, up to 600μ long, with very short branches, which are usually 1-5, sometimes up to 10 cells long, second or scattered, cells $6.5-9.5\mu$ diameter, $9.5-19\mu$ long; hairs absent, occasionally the terminal cells gradually much tapered toward the end, but containing chromatophores; chromatophore single, parietal, with a prominent central pyrenoid; monosporangia obovoid, sessile or with a 1-cell stalk, 1 or 2 on each articulation, terminal or second, very rarely otherwise, in crowded groups on short branches, $8.0-9.5\mu$ diameter, (13-) $16-19\mu$ long; occasionally replaced by bisporangia.

This species differs from *Acrochaetium Daviesii* (Dillwyn) Naegeli in having a strongly marked endozoic habit and very short lateral branches. In size and habit it is near to *Acrochaetium endozoicum* (Darbishire) Hamel, but *A. endozoicum* has shorter free filaments with copiously forked branches as shown in Darbishire's drawings, and much shorter monosporangia.

Found on *Alcyonidium Mytili* Dalyell, washed ashore in Sheep Pen Harbor, Sept. 1, 1934. Type in C.-C. Jao collections and Herb. Univ. Mich., Woods Hole No. 279.

Acrochaetium Alcyonidiae Jao var. *cylindricum*, var. nov.

(Pl. 12, fig. 5)

Filamentis endozoicis $5.0-6.5\mu$ latis, cellulis $6.5-13\mu$ longis; filamentis erectis ad 300μ altis, cellulis $4-5\mu$ latis, $10-19\mu$ longis; ramulis lateralibus

brevissimis, longitudine 1-4-cellulis; monosporangiis cylindrico-obovoideis, plerumque terminalibus, raro lateralibus, $4.0-6.5\mu$ latis, $9.5-13\mu$ longis; ceterum forma typica similis.

Endozoic filaments $5.0-6.5\mu$ diameter, the cells $6.5-13\mu$ long; erect filaments up to 300μ tall, cells $4-5\mu$ diameter, $10-19\mu$ long; branches very short 1-4 cells long; monosporangia cylindric-obovoid, usually terminal, rarely lateral, $4.0-6.5\mu$ diameter, $9.5-13\mu$ long; otherwise as in the type species.

This variety differs from the type form of the species in having all cells of lesser dimensions and the cylindric-obovoid monosporangia mostly terminal on the very short branches. It also bears some resemblance to *A. strictum* (Rosenvinge) Hamel and *A. gracile* Børjesen, but differs from both in having an endozoic habit; furthermore, the first has greater dimensions of all cells, the branches are longer and hairs are present, and the second has filaments with long branches which taper toward the tip and often end in long hair-like prolongations, and has larger sporangia.

Growing on *Alcyonidium Mytili* Dalyell mixed with *Acrochaetium Alcyonidiae* Jao, and partly endozoic, washed ashore in Sheep Pen Harbor, Sept. 1, 1934. Type in C.-C. Jao collections and Herb. Univ. Mich., *Woods Hole No. 279: B.*

***Acrochaetium radiatum*, sp. nov.**

(Pl. 10, figs. 18-25)

Thallo epiphytico, prostrato, ferme orbiculato vel irregulare, altitudine ad 320μ ; spora germinante in duas cellulas plus minusve aequales divisa, ex quibus 3-6 (raro ultra) fila ramosa repentes procreantibus, plus minusve radiatis compositibus; filis abunde ramosis, ramulis ad media pars thalli plerumque oppositis et dense compositis, forma pseudo-parenchymaticis, ramulis ad apicem filiorum plerumque furcatis vel secundis et fluxis; cellulis $5.0-6.5\mu$ altis, $6.5-9.5\mu$ longis; ramulis erectis non visis vel tenuiter procreantibus, solum 1- vel 3-cellularibus; chromatophoro parietali, pyrenoideo centrali; pilis terminalibus, plerumque in filis erectis; monosporangiis in filis prostratis, singulis et sessilibus, raro 1 vel 2 in filis erectis terminalibus, ovatis, (5-) $6.5-8.0\mu$ altis, $8.0-9.5\mu$ longis.

Plants epiphytic, prostrate on the host, almost circular in form or irregular, up to 320μ broad; the germinating spore dividing into two nearly equal cells, from which are produced 3-6 (or rarely more) main filaments in all directions in a single plane, resulting in a more or less regularly radiate arrangement of the filaments; abundantly branched, the branches near the center usually opposite and densely arranged, resulting in a pseudo-parenchymatous appearance, the branches near the end of the main filaments often dichotomous or secund and loose, their cells $5.0-6.5\mu$ diameter, $6.5-9.5\mu$ long; erect branches absent or poorly developed, only 1-3 cells long; chromatophore parietal, with a central pyrenoid; hairs terminal, mostly on erect filaments;

monosporangia directly produced on the prostrate filaments, or sometimes 1 or 2 terminal on the erect branches, oval in form, (5-) 6.5-8.0 μ diameter, 8.0-9.5 μ long.

These plants bear some characteristics of *Acrochaetium reductum* (Rosenvinge) Hamel, *A. humile* (Rosenvinge) Børgeesen and *A. pulchellum* Børgeesen, but differ from them chiefly in having more than two main filaments arising from the divided germinating spore and all the filaments arranged radiately and densely from the center of a fully developed thallus. Beside these characteristics, this new species is separated from the last two especially by the absence of stellate chromatophores. *Acrochaetium maculum* (Rosenvinge) Hamel also has a circular frond which is composed of more or less regularly radiating filaments and is pseudo-parenchymatous in appearance, but it has stellate chromatophores and a different method of spore germination.

Found on *Polysiphonia fibrillosa* Grév., together with several other species of *Acrochaetium*, Norton Point, Marthas Vineyard, Massachusetts, Aug. 3, 1934. Type in C.-C. Jao collections and Herb. Univ. Mich., *Woods Hole No. 280*.

ACROCHAETIUM EMERGENS (Rosenvinge) Hamel

(Pl. 13, figs. 7, 7B)

Vegetative filaments wholly endophytic in the cuticular layer of the host plant, horizontally extended; branches generally given off from the main filaments at right angles; cells varying in shape, mostly swollen in the middle, 1.5-3.5 μ diameter, 9.5-12.8 μ long; chromatophore parietal, occupying a large part or filling the cell, pyrenoid apparently absent; monospores terminal on a 1-cell stalk, and entirely free from the host, or sessile and endophytic, oval in form, 3.2 μ diameter, 4.5-5 μ long.

This local form is quite similar to Rosenvinge's type, except for a little difference in size. It is a new record for North America, and was found in *Polysiphonia fibrillosa*, from Norton Point, Marthas Vineyard, Massachusetts, Aug. 3, 1934.

Cruoriopsis Ensisae, sp. nov.

(Pl. 13, figs. 3-6)

Thallo horizontaliter expando, lineamento irregulari, usque ad 3 mm. diametro, strato basali monotromatico e filis radiantibus approximatis composito, crassitudine 13-19 μ ; ramulis dichotomis, cellulis aspectu superficiali quadrangulatis vel oblongis, raro triangulatis, (3.2-) 6-11 μ latis, 6-16 μ longis; per temporam fructiferam filamentis erectis basi dispositis procreantibus, longitudine 2- vel 4-cellularibus, cellulis 6.5-9.5 altis, 9.5-13 μ longis; chromatophoris nonnullis continentibus, colore roseo, parietalibus, disciformi-

bus; tetrasporangiis in filis erectis 1-cellularibus terminalibus, inter filas sterillas, ovatis, 16–25 μ altis, 22–35 μ longis, irregulariter cruciatim divis; partes sexuales ignoti.

Fronds horizontally expanded, irregular in outline, up to 3 mm. in diameter, 13–19 μ thick; filaments mostly dichotomously branched, appressed to each other to form the basal layer; cells square or oblong, rarely triangular in surface view, (3.2–) 6–11 μ diameter, 6–16 μ long; during the fruiting stages the erect filaments two or four cells long arise from the basal layer in groups, their cells 6.5–9.5 μ diameter, 9.5–13 μ long; several rose-colored parietal disc-shaped chromatophores in each cell; tetrasporangia produced among the free filaments, on stalks of one cell, ovate, 16–25 μ diameter, 25–32 μ long, irregularly cruciate divided to form the tetraspores; sexual reproduction unknown.

It is unfortunate that the sexual organs of this species were not found in the writer's collections. His determination was based upon the tetrasporangial plants, which showed the characteristic encrusting monostromatic basal layer and the irregularly cruciate tetrasporangia terminal on short stalks between the sterile erect filaments, which are features quite similar to the genus *Cruoriopsis*, but these plants differ from the type and other species of that genus in having the erect filaments in groups on the basal disc and the cells containing several disc-shaped chromatophores. This terminal tetrasporangium is also found in the genus *Rhododiscus*, but all the erect filaments of *Rhododiscus* are terminated by the tetrasporangia, i.e., sterile erect filaments are absent. *Cruoriopsis hyperborea* Rosenvinge reported from Ellesmere Land has thicker crusts, longer sterile erect filaments and much smaller tetrasporangia.

Plants were found on the empty shell of *Ensis directus*, mixed with *Conchocelis rosea* Batters and *Ostreobium Quecketii* Born. and Flah., dredged from 25 feet depth of water between Gay Head, Marthas Vineyard and Cuttyhunk Island, Massachusetts, July 17, 1934. Type in C.-C. Jao collections and Herb. Univ. Mich., *Woods Hole No. 281: B.*

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Explanation of plate 10

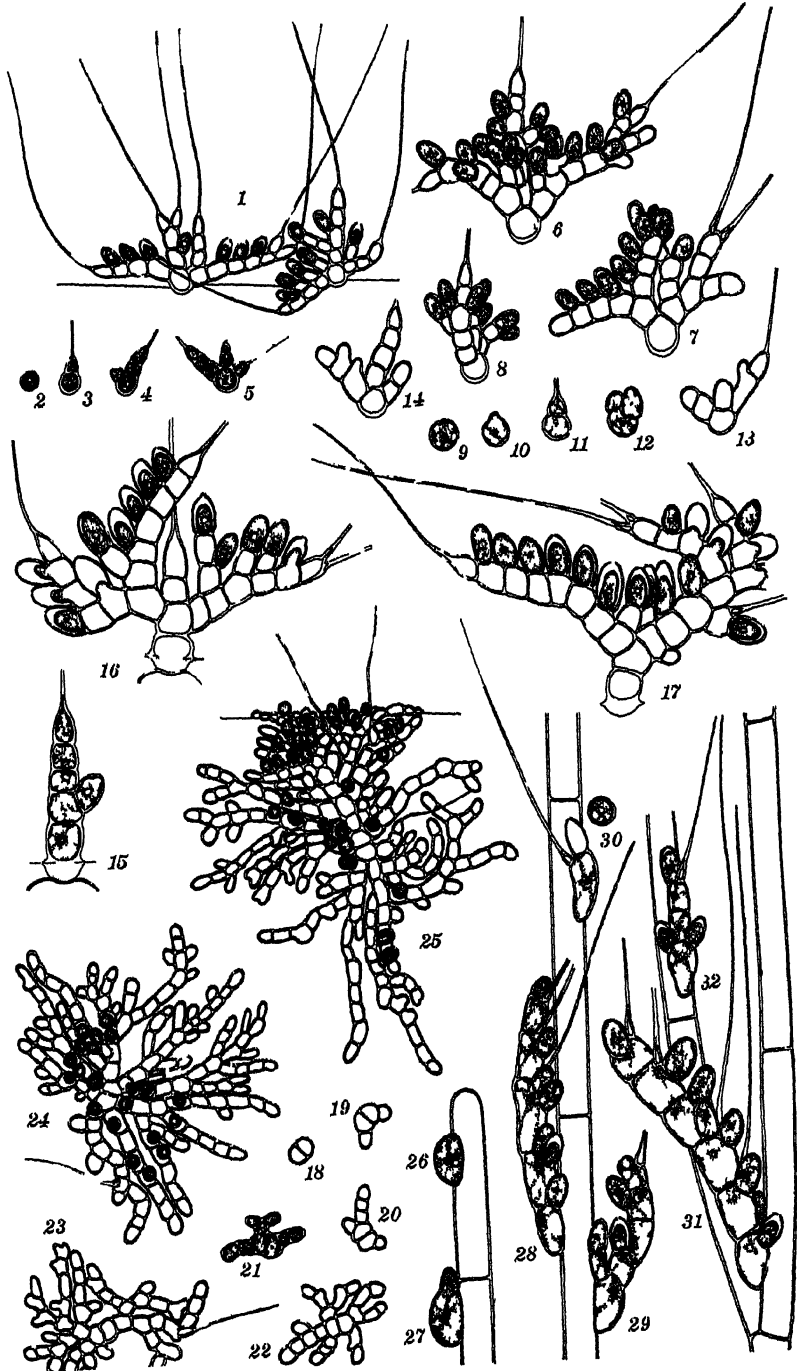
Figs. 1-5. *Acrochaetium microfilum* Jao, sp. nov. $\times 605$. Figure 1, two fully developed plants; figures 2-5, four young plants, showing the earliest developmental stages.

Figs. 6-14. *Acrochaetium compactum* Jao, sp. nov. $\times 605$. Figures 6-8, three well developed plants in different views; figures 9-14, young plants, showing the developmental stages.

Figs. 15-17. *Acrochaetium moniliforme* (Rosenvinge) Børgesen var. *Mesogloiae* Jao, var. nov. $\times 605$. Figure 15, a young plant, showing the earliest ramification, stellate chromatophores, and the much thickened lower wall of the basal cell immersed in the mucilage layer and attached to the peripheral cell of the host; 16 and 17, two adult plants.

Figs. 18-25. *Acrochaetium radiatum* Jao, sp. nov. $\times 605$. Figures 18-23, developmental stage of young plants; figures 24-25, two adult plants.

Figs. 26-32. *Acrochaetium unifilum* Jao, sp. nov. $\times 605$. Figure 26, an undivided germinating spore; figure 27, a germinating spore, showing the earliest stage of the first articulation of the erect filament arising from the upper lateral side of the monospore; figure 30, a dwarf plant composed only of a basal cell, a monosporangium and a hair, the monospore freed from the monosporangium just before drawn; figures 28-29 and 31-32, adult plants in different forms.

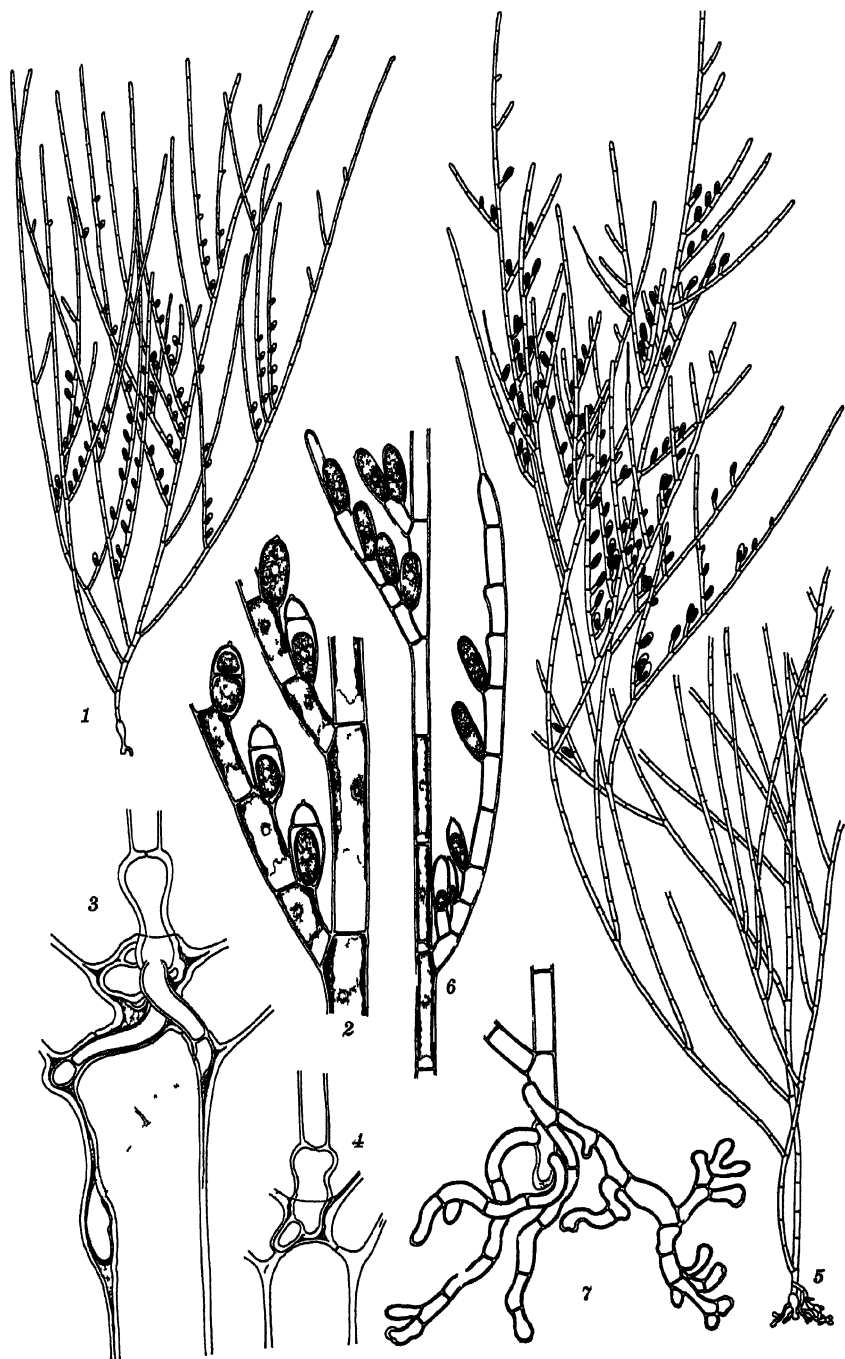


100 RHODOPHYCEAE

Explanation of plate 11

Figs. 1-4. *Acrochaetium intermedium* Jao, sp. nov. Figure 1, habit drawing of an adult plant, $\times 84$; figure 2, part of the plant, showing the structures of vegetative cells and bisporangia, $\times 605$; figures 3-4, basal parts of the plants, showing the intra-membranal habit, $\times 605$.

Figs. 5-7. *Acrochaetium subseriatum* Jao, sp. nov. Figure 5, habit drawing of an adult plant, $\times 84$; figure 6, detail of branchlets bearing monosporangia, showing ripe and regenerating sporangia and chromatophores, $\times 360$; figure 7, detail of holdfast, $\times 360$.



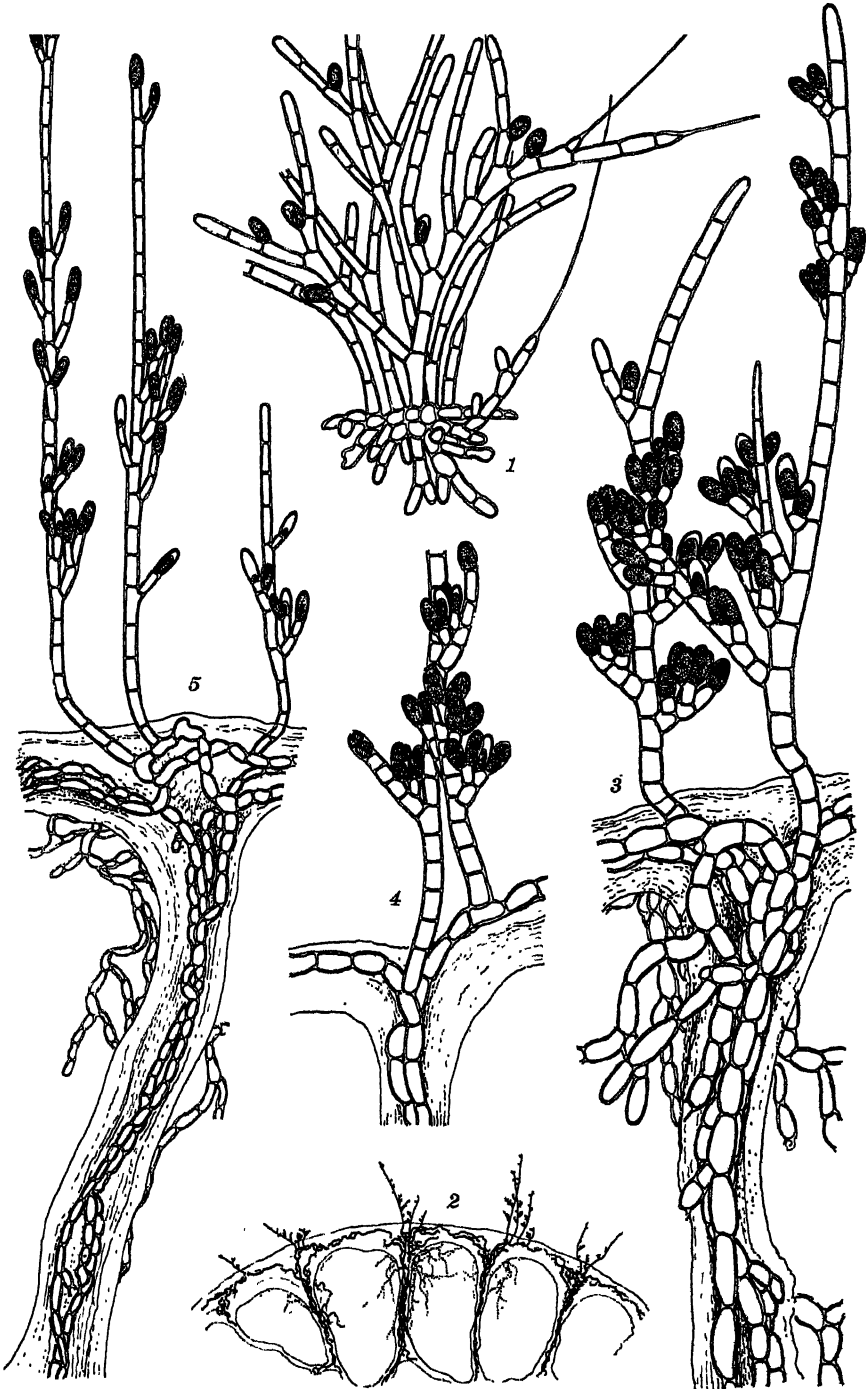
JAO RHODOPHYCEAE

Explanation of plate 12

Fig. 1. *Acrochaetium attenuatum* (Rosenvinge) Hamel, $\times 360$.

Figs. 2-4. *Acrochaetium Alcyonidiae* Jao, sp. nov. Figure 2, cross section of *Alcyonidium Mytili* Dalyell, showing the endozoic habit of the *Acrochaetium* plants, $\times 42$, figure 3, detail of adult plants, $\times 360$, figure 4, adult plant, showing the bisporangia and part of the epizoic basal filament, $\times 360$.

Fig. 5. *Acrochaetium Alcyonidiae* Jao var. *cylindricum* Jao. var. nov. $\times 360$.



JAO: RHODOPHYCEAE

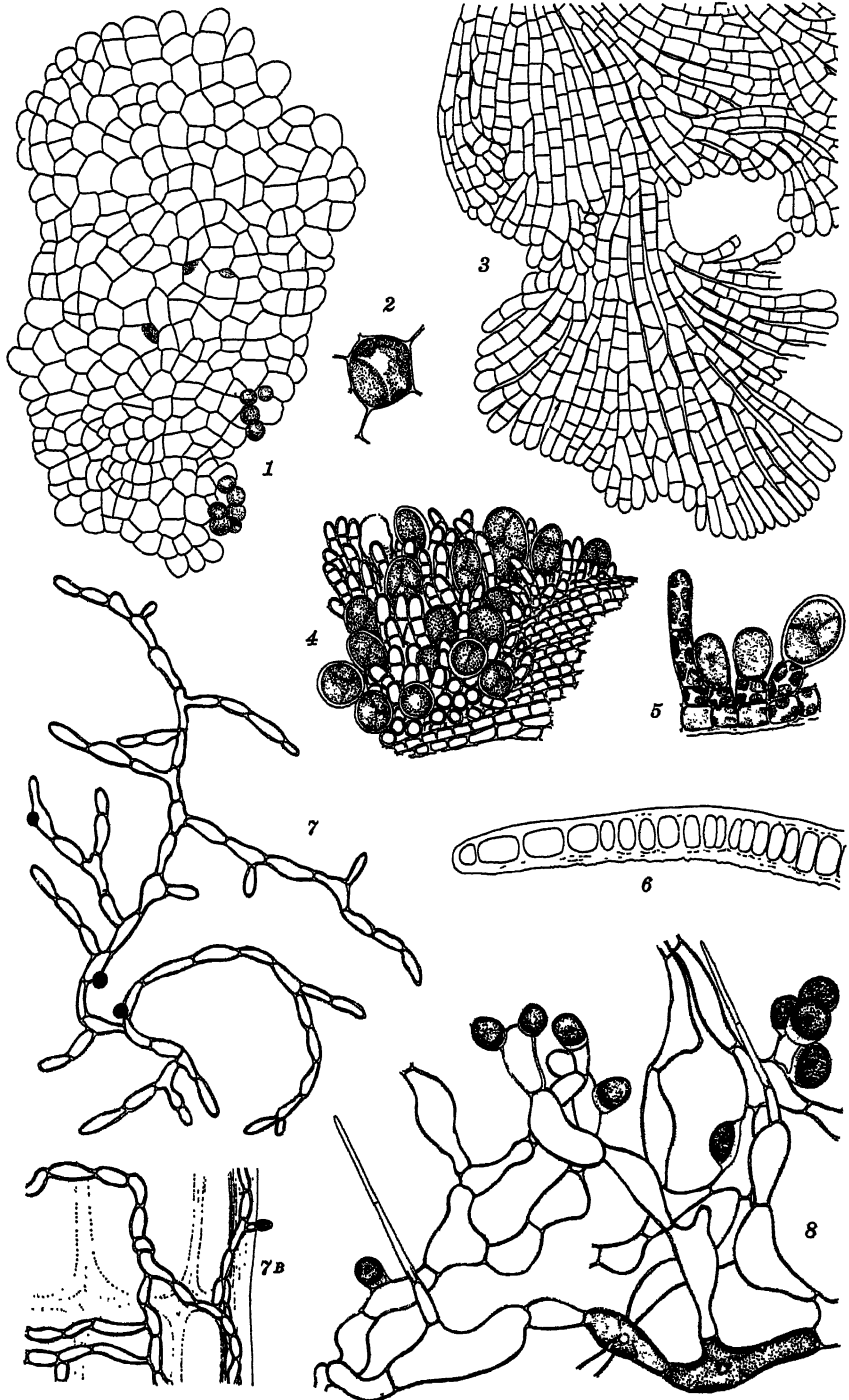
Explanation of plate 13

Figs. 1, 2. *Erythropeltis discigera* Schmitz var. *Flustrae* Batters. Figure 1, habit of fruiting plant, $\times 360$, figure 2, detail of fruiting cell, showing formation of monospore and structure of chromatophore, $\times 750$.

Figs. 3-6. *Cruoriopsis Ensissae* Jao, sp. nov. Figure 3, part of the plant, showing arrangement of filaments, ramification, and irregularly lobed margin of thallus, $\times 360$, figure 4, detail of fruiting portion, showing tetrasporangia scattered among the sterile filaments, $\times 360$, figure 5, cross section of fruiting portion, showing 1-cell stalked tetrasporangia and sterile filament and chromatophores, $\times 605$, figure 6, cross section of margin of thallus, $\times 605$.

Figs. 7, 7B. *Acrochaetium emergens* (Rosenvinge) Hamel. $\times 605$. Figure 7, habit of fruiting plant, figure 7B, part of thallus, showing the endophytic filaments and a free, 1-cell stalked monosporangium.

Fig. 8. *Colaconema americana* Jao, sp. nov. $\times 605$. Part of interweaving, fruiting thallus bearing sporangia in different forms and positions, and cylindrical free filaments.



JAO: RHODOPHYCEAE

A study of blossom bud differentiation in the McIntosh variety of apple¹

ISADOR AARON

(WITH PLATES 14 AND 15)

The work herein reported was conducted during the growing season in 1931, to investigate the possible correlation between the morphological condition of the primordial meristem and blossom bud development; and the possible correlations between such treatments as nitrate application, girdling and scoring of the trees and blossom bud development. This was done in order to develop an indicator which would enable one to determine much earlier in the season than had been possible before, which buds would become blossom buds and which buds would become vegetative buds. The principal morphological character used for this purpose was the breadth of the primordial meristem. Spur buds alone were studied, since the process of differentiation is similar for both the spur bud and the axillary buds of the apple tree.

METHODS

In the present study, buds were taken from the McIntosh variety of apple. The trees were budded on ordinary French crab seedlings, used as rootstocks. Only buds from spurs two or more years old were used. The buds were prepared for study by the paraffin method, and stained with Flemming's triple stain. To eliminate xylol and the higher grades of alcohol *n*-butyl alcohol was used. Continued soaking in paraffin for as long as a year made microtome work easier. A sliding microtome was used, to secure sections around 10 μ thick. The meristem breadths of the buds removed up to and including July 14 were measured in microns. The breadth of the buds removed up to and including July 14 were measured in microns. The breadth of the primordial meristem was considered to be the distance between the bases of the nearest scales occurring on opposite sides of the meristem.

By random selection, the buds were removed from six selected trees at intervals of 4-7 days, on and between May 2 and July 14, on July 29, and September 18, 1931. Two of the trees were girdled, the girdle being 5-10 mm. wide, two of the trees were scored with two sharp knife cuts, and two were uncut. The girdled and scored trees were treated in this way each year for three years preceding the beginning of this study. On March 17, 1931,

¹ Joint Contribution from the Departments of Botany (No. 98) and Horticulture, Pennsylvania State College, State College, Pa. Authorized for publication on January 28, 1936, as paper No. 724 in the Journal Series of the Pennsylvania Agricultural Experiment Station.

sodium nitrate was applied to one girdled tree, one scored tree and one uncut tree. The girdling and scoring were done June 8, 1931. Buds were opening May 2. By June 24, bud scales were visible to the naked eye, on the terminal buds. Since there were primordia of blossoms in some of the buds removed July 29, and flower clusters in some of the buds removed September 18, these buds were used only for morphological studies.

Selected meristems were used for photomicrographs. A magnification of $150\times$ was used for meristems alone, and one of $73\times$ for other details.

RESULTS

The percentage of spur blossom buds on each of these trees was determined by actual count, the following spring. This percentage, given in table 1, is the proportion of these spur buds remaining on the tree, after

TABLE 1

Statement concerning buds removed from and left on tree, and blossom buds on tree at blooming time, 1932

TREE	TOTAL NO. OF BUDS ON TREE	NO. OF BUDS LEFT AFTER SAMPLING WAS COMPLETED	% OF BLOS- SOM BUDS, FOUND BY ACTUAL COUNT IN SPRING OF 1932	NUMBER AND PER CENT OF TOTAL BUDS IN SAMPLES AT PERIODS STATED							
				MAY 2 TO JUNE 8		JUNE 12 TO JUNE 24		JUNE 29 TO JULY 14		MAY 2 TO JULY 14	
				NO.	%	NO.	%	NO.	%	NO.	%
Ungirdled minus nitrates	1024	793	42.0	67	6.5	88	8.6	76	7.4	231	22.5
Girdled minus nitrates	1693	1497	79.3	61	3.0	62	3.0	73	4.3	196	11.5
Girdled plus nitrates	1435	1223	42.8	58	4.0	74	5.1	80	5.6	212	14.7
Scored minus nitrates	1044	853	74.9	69	6.6	59	5.7	63	6.0	191	18.3
Scored plus nitrates	1221	1008	39.7	64	5.2	62	5.1	87	7.2	213	17.4
Ungirdled plus ni- trates	1613	1395	66.1	68	4.2	74	4.6	76	4.7	218	13.5

sampling was completed in 1931, that opened in the spring of 1932 to produce bloom. In this table the buds collected at shorter intervals were combined, so that those collected between May 2 and June 8 constitute one sample, those collected from June 12 to June 24 a second sample, and those collected from June 29 to July 14 a third sample. In this table the treatment of the tree, the total number of buds on the tree at the beginning

TABLE 2
Meristem breadths and blossom production

TREE	% BLOSSOM BUDS BY ACTUAL COUNT	BREADTH OF MERI- STEMS (MICRONS)	PER CENT OF TOTAL BUDS MEASURED WHICH WERE AT OR ABOVE THE MICRON BREADTH INDICATED			
			MAY 2- JUNE 8	JUNE 12- JUNE 24	JUNE 29- JULY 14	MAY 2- JULY 14
Ungirdled minus ni- trates check	42.01	130	62.7	73.9	89.5	75.5
		140	56.7	64.8	86.8	69.7
		150	40.3	50.0	68.4	53.2
		160	35.8	45.4	60.5	47.6
		170	25.4	35.2	52.6	38.1
		180	23.9	28.4	47.3	23.3
		190	16.4	19.3	35.5	23.8
		200	14.9	13.6	31.6	19.9
Girdled minus nitrates	79.29	130	86.8	91.9	98.6	92.9
		140	81.9	87.0	98.6	89.8
		150	68.8	85.5	97.3	84.7
		160	62.3	79.0	93.2	79.1
		170	54.0	66.1	84.9	69.4
		180	39.3	58.0	75.3	58.7
		190	36.0	48.4	67.1	51.5
		200	32.8	33.8	53.4	40.8
Girdled plus nitrates	42.76	130	70.7	72.9	91.3	79.2
		140	67.2	66.2	88.8	75.0
		150	48.3	48.6	70.0	56.6
		160	39.7	37.8	66.3	49.0
		170	27.6	25.7	52.5	36.3
		180	20.7	24.3	46.3	31.6
		190	15.5	12.2	42.8	21.2
		200	13.8	10.8	26.3	17.5
Scored minus nitrates	74.91	130	81.1	88.1	98.4	89.0
		140	69.6	88.1	96.5	84.3
		150	65.2	76.3	88.9	76.4
		160	60.9	66.1	74.6	67.0
		170	49.3	54.2	54.0	52.4
		180	39.1	47.5	44.4	43.5
		190	27.5	33.9	33.3	31.4
		200	24.6	15.2	22.2	20.9
Scored plus nitrates	39.68	130	71.8	80.6	90.8	82.1
		140	62.5	69.3	87.3	74.6
		150	45.3	46.8	66.7	54.5
		160	43.7	43.5	64.4	52.1
		170	31.2	33.9	51.7	40.4
		180	28.1	30.6	47.1	36.6
		190	24.3	25.8	39.1	30.5
		200	18.7	25.8	28.7	24.9

TABLE 2 (Continued)

TREE	% BLOSSOM BUDS BY ACTUAL COUNT	BREADTH OF MERI- STEMS (MICRONS)	PER CENT OF TOTAL BUDS MEASURED WHICH WERE AT OR ABOVE THE MICRON BREADTH INDICATED			
			MAY 2- JUNE 8	JUNE 12- JUNE 24	JUNE 29- JULY 14	MAY 2- JULY 14
Ungirdled plus nitrates	66.09	130	75.9	94.6	92.2	88.0
		140	63.2	89.2	85.9	80.7
		150	48.5	71.6	78.9	67.0
		160	45.6	67.6	73.7	62.8
		170	30.9	55.4	64.5	50.9
		180	27.9	45.9	61.8	45.9
		190	25.0	31.1	55.3	37.6
		200	23.5	27.0	47.4	33.0

of the study, the percentage of this total removed for each sample, and the number of buds remaining on each tree are also given.

In table 2 are given the results of the measurements of the meristem breadths. An examination of the data presented in this table indicates a correlation between the breadth of the meristem and the number of blossom buds formed. These meristems increase in breadth as the growing season advances. There is a definite tendency for the correlation between the breadths of the primordial meristems and the percentage of blossom buds to occur at ever greater breadths through the growing season. The increase in breadth of these meristems is a continuous progression from the beginning of the growing season until the appearance of primordia of blossom clusters later in the summer. The primordial meristems that will differentiate into blossom clusters are most likely broad meristems.

Table 3 presents the results of statistical analysis. For each sample and for the total meristems removed from each tree, the mean of the breadth measurements is given. In each case the significance of the mean of each treated tree, as compared with the mean of the uncut tree not treated with nitrates, is given. The uncut tree not treated with nitrates is considered as a check. When compared with the mean of the check, the significance of the mean of the treated tree can be found.

The data of table 3 indicate that, while the mean of the breadths is greater with each successive sample of buds, this increase seems to occur without any relationship to treatment. In regard to significance of such treatments as girdling or the use of nitrates the results seem too variable for an inference to be made.

In the process of study of the morphology of the meristems, a line is drawn to connect the bases of the nearest scales. This line is called a chord. The depth of the meristem is the distance from the crest of the meristem

to the chord. Data on the examples cited are presented in table 4, and consist of measurements of these meristems.

In relation to the morphology of these meristems, the provascular form, the changes in form of the primordial meristem, and the primordia that arise from it in the process of blossom bud differentiation were studied. The provascular form is the ring of procambium strands surrounding the pith at the tip of the fruit spur. While the number of layers of cells in the meristem were too variable to be used as an indicator, changes in the shape of the provascular form and in the form and depth of the meristem were of value in the study of blossom bud differentiation.

TABLE 3

Significance of the means of meristem breadth measurements of treated trees

TREE	MAY 2-JUNE 8			JUNE 12-24			JUNE 29-JULY 14			MAY 2-JULY 14		
	BUDS STUDIED	MEAN IN μ	SIGNIFICANCE	BUDS STUDIED	MEAN IN μ	SIGNIFICANCE	BUDS STUDIED	MEAN IN μ	SIGNIFICANCE	BUDS STUDIED	MEAN IN μ	SIGNIFICANCE
Ungirdled minus nitrates check	67	145.4	—	88	156.8	—	76	175.5	—	231	159.7	—
Girdled minus nitrates	61	177.1	6.8	62	186.5	7.5	72	206.9	7.6	196	191.1	12.3
Ungirdled plus nitrates	68	159.7	3.2	74	161.4	1.3	74	192.4	4.4	218	175.9	6.4
Scored plus nitrates	64	153.6	1.8	62	164.3	1.7	87	176.8	0.3	213	166.8	3.0
Scored minus nitrates	69	168.4	5.3	59	174.2	4.4	63	177.1	0.4	191	173.1	5.6
Girdled plus nitrates	58	168.3	5.2	74	152.4	1.3	80	173.0	0.6	212	160.0	0.1

In the process of blossom bud differentiation the shape of the provascular form, and the form of the primordial meristem, constantly change, and the depth of the meristematic mass increases. The author has divided this process of change in dimensions and visible form into arbitrary stages. While a leaf or scale is being produced from the primordial meristem, the outline of the meristem is a flat, more or less broken line. This is stage 1 (pl. 14, fig. 1). After the primordium of the scale or leaf is produced, the flat broken outline of the primordial meristem disappears and changes into the form of the arc of a circle. Cell division seems to fill in the arc. Stage 2 (pl. 14, fig. 3) represents this condition.

In stage 3 (pl. 14, figs. 4, 6; pl. 15, fig. 1) the primordial meristem undergoes a series of changes. Though the arc-like form of the meristem is retained for an interval, the margin of the meristem outline develops a curve of its own, so that the arc-like form seems to rest upon the upper boundary of the margin. Finally, cell division away from the center tends to reduce the curvature of the meristem to such a degree that the meristem resembles

a plateau with long and steep slopes. The arc-like curvature has been constantly disappearing until the plateau has been formed. With more cell division, the flat upper surface of the plateau becomes distorted, and the slopes of the plateau become obscured as the distortion proceeds. The depth of the primordial meristem constantly increases, and the distortion becomes greater, until this meristem is a large distorted mass of tissue (pl. 14, fig. 6; pl. 15, fig. 1).

The provascular form is hemispherical in the first two stages and the early part of stage 3 (pl. 14, fig. 2). As the form of the meristem becomes distorted, the shape of the provascular form becomes more conical. When the primordial meristem has become a distorted mass of tissue the provascular form is broadly conical in shape.

In the production of leaves and scales all primordial meristems pass through the first two stages and the early part of stage 3. The primordial meristem does not assume the form of a plateau. Preceding the appearance of a scale or a leaf, the meristem becomes deeper and more arc-like. Following this appearance, the meristem is shallow, with its surface a more or less flat broken plane. The appearance of each scale and leaf primordium seems to be preceded and followed by this sequence of events. The provascular form is always hemispherical in shape.

Until the primordial meristem enters stage 4 it is a simple mass of tissue. After the meristem enters this stage, primordia of blossoms arise from it. By a process of separation and cell division a succession of primordia forms (pl. 15, figs. 2, 3, 5). For the sake of clarity it can be assumed that the primordial meristem has ceased to exist, being transformed into primordia. There are formed a terminal (central) primordium and lateral primordia. The lateral primordia become leaves or bracts. From the sides of the terminal primordium arise more lateral primordia as the terminal primordium retains its identity, and, by cell division, increases in volume and dimensions. Finally, after a number of leaves or bracts have been produced, the terminal primordium develops into a terminal blossom, while each of the most recently developed lateral primordia develops into a lateral blossom, each lateral blossom being in the axil of a bract.

From the first alteration of the deep, broad and distorted primordial meristem into the terminal primordium and the first lateral primordia, until the most recent primordia become blossoms, the sequence of the appearance of the primordia is a matter of repetition. Until the terminal primordium becomes a blossom, there is always a terminal primordium 80–150 μ broad to continue the process of generation. The appearance of the blossoms represents the completion of a developmental progression.

With this process of change from the distorted primordial meristem

into a blossom cluster, the provascular form has changed from a shape broadly conical to one that is a long attenuated cone.

In table 4 measurements of the examples cited are given. They merely illustrate the point that a primordial meristem increases in breadth and

TABLE 4
Dimensions of meristems and primordia

		MICRONS BREADTH OF		DEPTH MICRONS	
		PRIMORDIAL MERISTEM	TERMINAL PRIMORDIUM		
14	1	136		13	1
14	3	260		42	2
14	4	240		64	3
14	6	240		123	3
15	1	265		147	3
15	2	247	150	167	4
15	3		80	143	4
15	5		150		4

depth while differentiating into a blossom cluster. No primordial meristems less than 220μ broad were observed to differentiate into blossom clusters.

DISCUSSION

Stating briefly the development of the flower cluster of the apple, Kraus (1913) writes that "the first observable indication of the flower is the more or less thickening of the axis. Minute bracts, in the axils of which are found blunt protuberances, arise from it in a very close spiral. The tip of the axis never loses its identity, but on the contrary enlarges considerably and always develops slightly in advance of the protuberances immediately below it. Later these protuberances develop into definite individual flowers."

Many workers, including Drinkard (1909-10), have attempted to recognize the early stages of blossom bud formation. It has been observed that first the growing point flattens, and then it thickens and rises above the bases of the nearest scales as the flower cluster is about to appear. Many disagree about the breadth of the primordial meristem as a criterion in the recognition of the early stages of blossom bud differentiation. The corrugation of the primordial meristem is considered by Drinkard as the earliest indication of blossom bud differentiation. Neither the breadth nor the rising of the meristem above the bases of the nearest scales before it becomes corrugated seem to be considered as matters of importance.

Much work has been done on the differentiation of flowers from meristems. This report deals with the diameter of the primordial meristem in

relation to the differentiation of the blossom bud of the McIntosh variety of apple. On the basis of the work done in this study, the following inferences seem justified by the results obtained. There is correlation between meristem breadth and blossom formation. The breadths increase from the time of bud break in the spring until flower buds begin to form and vegetative buds become dormant. Flower buds probably develop from broad meristems.

Breadth is a relative term. A primordial meristem considered broad on May 8 may not be considered broad on July 7. Breadth is related to time, and should be considered in terms of range rather than precise size. Primordial meristems that differentiate into blossom buds are probably even broader than the data of table 2 would indicate. For blossom clusters to differentiate, the primordial meristems must be of a breadth of at least 220μ .

There is a tendency for the mean of the breadths of the primordial meristems to increase in succeeding sampling periods. There was too much variation in the statistical data for a statement on the effects of the treatments to be made. The results of statistical analysis do not deny that treatment may influence fruit bud formation. They merely indicate the danger of relying on too few trees for evidence. The results of culture, as girdling or nitrate application, can be governed by the number of individuals treated. In several cases the author observed variations in the number of flower clusters on different limbs of the same tree, even on some girdled trees. With a small number of trees, injury and biennial bearing might influence results when differences in culture are compared.

A division of blossom bud formation into a series of stages is possible. Though arbitrary, these stages illustrate a continuous process of development. All primordial meristems pass through stages 1 and 2, and through the early part of stage 3. The differences consist of events that happen afterward.

Concerning the breadth of the primordial meristem from which a blossom cluster will be differentiated, opinion is divided. Black (1916), Kirby (1918), and Goff (1899) state that the development occurs when a broad meristem is present. They believe that in the vegetative bud the growing point is narrow (Goff, 1899); that the inflorescence will develop from a broad growing region (Black, 1916); that when flower bud differentiation is occurring, the meristem thickens, its crest rises above the bases of the nearest scales, and its outline becomes irregular (Goff, 1899). Kirby (1918) reported that, in the apple varieties he studied, the crown of a leaf bud was found to be less than 0.14 mm. while the crown of a flower bud was 0.27 mm. broad during the period of flower bud differentiation.

Many workers believe that a broad primordial meristem is not a reliable indicator of blossom bud differentiation (Bradford, 1915; Magness, 1916; Rasmussen, 1930). They place more reliance on a narrow meristem as an indicator of this differentiation. In the consideration of such a matter as broad and narrow, the determination must first be made of what dimension is broad and what dimension is narrow.

Believing that there has been confusion regarding the "first stage of fruit bud formation," Bradford (1915) considers the matter in detail. He states that the undifferentiated crown "must be regarded as potentially either a leaf bud or a fruit bud." Though some have considered this "as the first stage in fruit bud formation," this structure is found at the tips of one-year-old twigs, and at times in early September. "Long before this time most buds have become differentiated into either leaf buds or fruit buds." He considers the differences between the buds. "Distinct leaf buds, well differentiated, were found as early as May. The leaf buds differ from the undifferentiated in that the crown is broader and flatter, is not raised so high above the level of the embryo leaves and scale bases, and has no swellings or very young leaves at its periphery. The amount of meristematic tissue is relatively less, and clearly defined tissue occurs closer to the growing point. All in all, the appearance presented strongly suggests a resting stage. Whether buds can advance from this resting stage again and form fruit buds in the same season is a matter for conjecture."

In contrast to Bradford the author believes that the so-called resting stage can occur at any time of the year. This is in stage 2. In this stage the meristem outline is like the arc of a circle. The flatness Bradford mentions seems to be the lack of a broken outline.

Such traits do not seem to be restricted to dormant buds. Other buds not in the dormant condition may have them. They may be present at any time, in an undifferentiated bud, a leaf bud producing leaves, a blossom bud in its earliest stages, or in a vegetative dormant bud.

This stage might be called a quiescent stage, to indicate that, at the moment, there is delayed morphological activity between the appearance of two successive primordia from a primordial meristem. The quiescent stage can be a matter of a day or of months. Furthermore, the quiescent stage is not correlated with blossom bud production. Primordial meristems of any breadth can be in this stage. In relation to this, the author believes that leaf buds can be differentiated at any time in the growing season.

There does seem to be some correlation between meristem depth and blossom bud development. Bradford is probably correct in believing that the meristems of undifferentiated and leaf buds seem to have less tissue, with undifferentiated tissue occurring closer to the growing point, and are

less raised above the nearest scale and leaf bases. Meristem depth as the chief criterion, however, can be misleading, for the breadth must be considered merely in relation to very broad meristems at the time visible differentiation of a blossom cluster is occurring.

Bradford also believes that the "first evidence of fruit bud formation" is "the rapid elevation of the crown into a narrow conical form, rounded at the apex, with fibrovascular connections and pith areas advancing concurrently." The succession of changes is rapid. In making this statement, Bradford may not have considered what seems to be the following sequence of events. After the primordium of a bract has formed, the broad primordial meristem has become a narrower terminal primordium. In the succession of lateral primordia following one another from a terminal primordium, with the terminal primordium finally becoming a terminal blossom, the terminal meristematic mass loses breadth and volume. While the breadth and volume of the terminal primordium will increase between the appearance of each preceding and following lateral primordium, events are too rapid for the former dimensions to be regained.

In the production of the lateral primordia of a blossom cluster, something more than cell division occurs. On the lateral portion of the terminal primordium an axis of cell division forms in a definite direction. By a partial separation, due to a kind of dichotomy, some of the lateral portion of the terminal primordium becomes a part of the lateral primordium. In leaf and undifferentiated buds the primordial meristems are not so raised and distorted that the formation of a lateral primordium near the margin is prevented.

The emphasis of Bradford seems to have been placed on the narrowed primordium rather than on the original primordial meristem. Though both resemble a truncated cone, the narrowed primordium is 80 to 150 μ broad, while the less raised primordial meristem is at least 220 μ broad, and is truncated nearer to the base.

Another factor might influence the difference of opinion. As distortion of the meristem occurs, the lower part of the margin differentiates into permanent tissue. Since the greatest breadth is between the bases of the nearest scales, emphasis might be placed on a narrow primordial meristem if the upper part only is considered.

The narrow portion is often broader than the meristems of leaf and undifferentiated buds. The data indicate that the blossom clusters will arise from meristems above a certain breadth range. Given a meristem at or near the lower limit of that range, and given the appearance of permanent tissue in the lower margin of the raised meristem, the illusion of narrowness can be held.

In his consideration of the process of blossom bud differentiation in the axillary buds of the apple, Magness (1916) writes "though a distinct raising and rounding of the crown was apparent" this was not fruit bud differentiation, for by July 9 "many buds had reached this degree of development without forming flower parts." Of the buds collected December 8, the crowns "were well differentiated and rounded evenly," with some "so well developed that had this condition been found earlier in the season they would almost certainly have been mistaken for blossom buds." Before this occurred, the recognition of the blossom bud was impossible. In reporting that the distinctly raised and rounded meristems were poor indicators of blossom bud differentiation, Magness ignored the possibility that competition between primordial meristems might occur. Some buds might be favorably located in regard to external factors. Others might be in a better position to receive the necessary substances. Since blossom bud formation is an exhausting process for the tree, there may not be enough material for primordial meristems that could produce flowers, to do so. Some might be prevented from becoming fruitful. The stage in which this prevention could occur might vary.

Once the process of blossom bud formation begins, it proceeds very rapidly. On any one tree (Kirby, 1918), most of the spur blossom buds form within a month of the time the first blossom buds form. Within the author's collections only the earliest visible stages are seen in the samples of July 14, while most of the stages up to a partial development of the terminal blossom are seen in those of July 29. Rapid differentiation and competitive action among the primordial meristems might account for the broad and merely arc-like meristems, and for those later stages seen by Magness. Furthermore, those who favor the narrow meristem as an indicator must account for the fact that meristems much less than 150μ broad can be found December 8.

Rasmussen (1930) does not believe that "the broadening of the floral axis, and the development of protuberances described by other investigators" can be considered blossom bud differentiation. He believes that Kirby's idea on the first indication of this differentiation was not clearly stated, and that Kirby (1918) may have confused leaf primordia with the earliest stages of flower bud differentiation. In his consideration of Kirby's work, it should be remembered that an apple flower bud is a mixed bud, with each lateral blossom produced in the axil of a bract. The leaves and bracts of the cluster are produced before the blossoms. The cluster arises from a greatly distorted meristem of at least 220μ broad. Kirby's presentation is not wrong.

The provascular form seems to be related to the kind of bud produced.

In leaf and undifferentiated buds it is more or less hemispherical, broken at the pole, where cells are not fully differentiated into permanent tissue. This form is retained in stages 1 and 2, and in the early part of stage 3. From then on, the provascular form changes progressively to and through the broadly conical shape, becoming ever more narrowly conical until a very long attenuated cone is present in the fully formed blossom bud. Though the provascular form may vary in each case, there is a definite tendency for it to become ever more conical. The reasons for this change in shape can merely be inferred. While the provascular form is hemispherical, the cells below the meristem seem to be enlarging at the same rate in all directions. After entering well into stage 3, the cell enlargement and cell addition seem to be more rapid in the direction of the longitudinal axis of the spur.

Since the differentiation of the primordial meristem seems to pass through the stages considered, and since this differentiation seems to occur only in the case of meristems at least 220μ broad, the broad primordial meristem can be considered as an indicator of later blossom bud differentiation. With this statement in mind, a person should be able to make an estimate, at any time in the growing season, of the proportion of blossom buds that will form.

The fate of a primordial meristem may be determined very early in the growing season. Differentiation into a blossom bud is probably determined long before the actual visible appearance of primordia of blossoms occurs. The causes of blossom bud differentiation must be determined. Both meristem breadth and blossom bud differentiation may be results of reactions preceding these events. Such matters as the type and time of treatment of the tree, and previous treatment of the tree, can probably influence the condition of the tree, and can probably aid or retard the conditions that are expressed in fruit bud differentiation.

Certain factors might intercede to alter the fate of a primordial meristem. Of many broad meristems competing for the necessary substances, some will lose out. Though treatment of the tree might alter the intensity of the competition, it would not prevent it; for on girdled trees vegetative spur buds occur, while on uncut nitrated trees broad meristems and blossom clusters appear.

There are many reports dealing with the time of blossom bud differentiation. The time range for trees like the apple has previously been considered to be between the last part of June and the last part of July. On the apple tree differentiation is said to occur earlier in spur than in axillary buds (Gibbs and Swarbrick, 1930; Magness, 1916). In an individual tree the period of differentiation may last a month (Kirby, 1918). In the pres-

ent trend of opinion, the dates of the visible differentiation of the blossom buds will be influenced by the variety, and by ecological factors including culture. The author agrees with Kirby² in the belief that the period of time within which most of the blossom buds form is more important than the earliest dates when differentiation into blossom buds occurs in the first buds to become blossom buds.

CONCLUSIONS

1. The breadth of the primordial meristem of apple buds, as indicated in this study, increases as the growing season advances.

2. There is a definite correlation between time and both the breadth of the primordial meristem and the differentiation of this meristem into a blossom bud.

3. The stages in the differentiation are passed through only after the primordial meristem has become very broad.

4. Rather than one resting stage in the bud of the apple tree, the present study indicates that there is a succession of quiescent stages, in which there is a decreased rapidity of morphological change. The quiescent stages can exist for different periods of time.

5. While the shape of the provascular form seems to be correlated with blossom bud differentiation, it is not as definite an indicator as meristem breadth.

6. One should be able to make a rough prediction, at any time in the growing season, as to the proportion of blossom clusters that will be formed.

7. Concerning the effects of the treatments of the individual, the results as expressed in blossom bud differentiation, were too variable for any inferences to be made.

ACKNOWLEDGMENT

The author is very grateful to the Department of Horticulture for financing this investigation, to Professor F. N. Fagan, of the Department of Horticulture, for his efforts in initiating the investigation, and for his continuous aid and interest; and to Dr. F. D. Kern and the other members of the botany department for the use of the laboratories in the course of this investigation. Without the valuable advice and constant helpfulness of Professors H. W. Popp, and H. W. Thurston, Jr., of the botany department, the progress of this investigation would have been impossible.

² A personal communication, August, 1934.

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Explanation of plates

High power photomicrographs are magnified 150 \times , while low power photomicrographs are magnified 72 \times . Dimensions are given in table 4.

Plate 14

Fig. 1. This is stage 1. A narrow undifferentiated primordial meristem in a condition of great activity. A primordium of a scale is being produced. The meristem outline is a more or less flat unbroken line.

Fig. 2. Same bud. The provascular form is hemispherical.

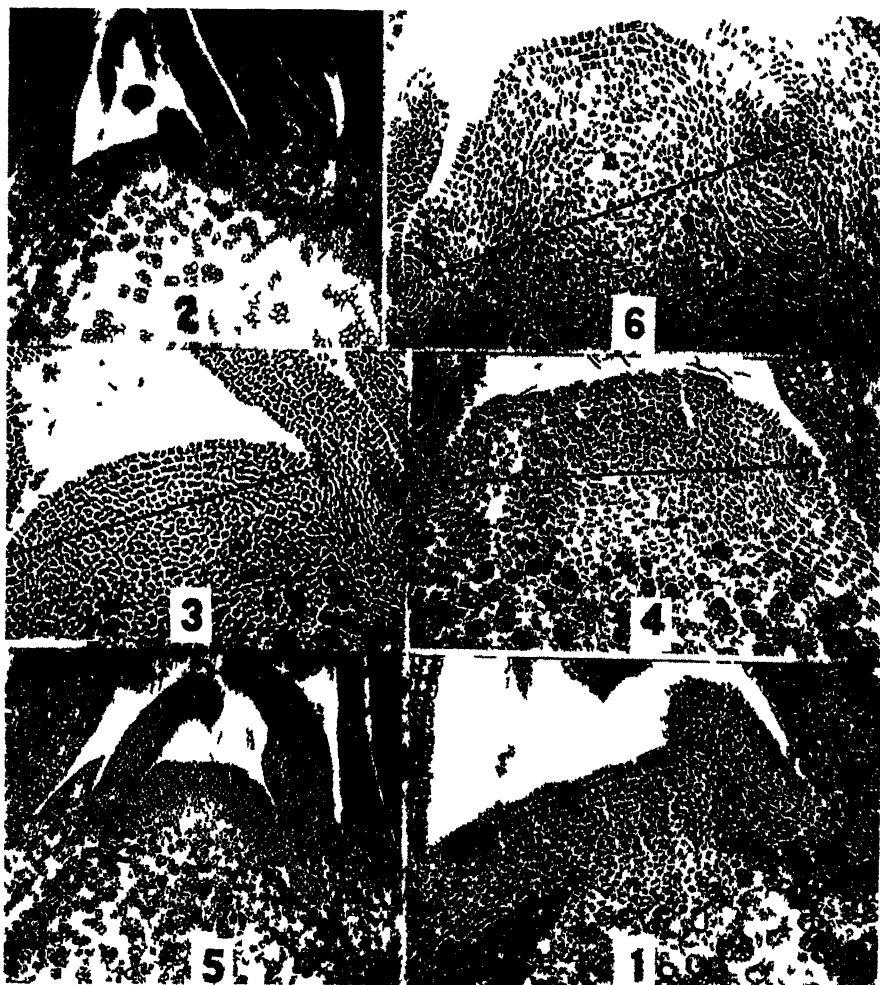
Fig. 3. This is stage 2. The primordial meristem is assuming the curve of an arc of a circle. The margin of the arc touches the bases of the nearest scales.

The following figures of plate 14, and plate 15, fig. 1 are in stage 3.

Fig. 4. The primordial meristem has lost its arc-like curve, and has assumed the form of a highly arched plateau. The meristem is becoming distorted.

Fig. 5. Same bud. The provascular form has become slightly conical.

Fig. 6. Same as plate 15, fig. 1.



AARON BUD DIFFERENTIATION

Plate 15

Fig. 1. The primordial meristem is a greatly raised and distorted mass of tissue.

The remaining figures of plate 15 illustrate stage 4. In this stage the primordial meristem has broken into individual primordia.

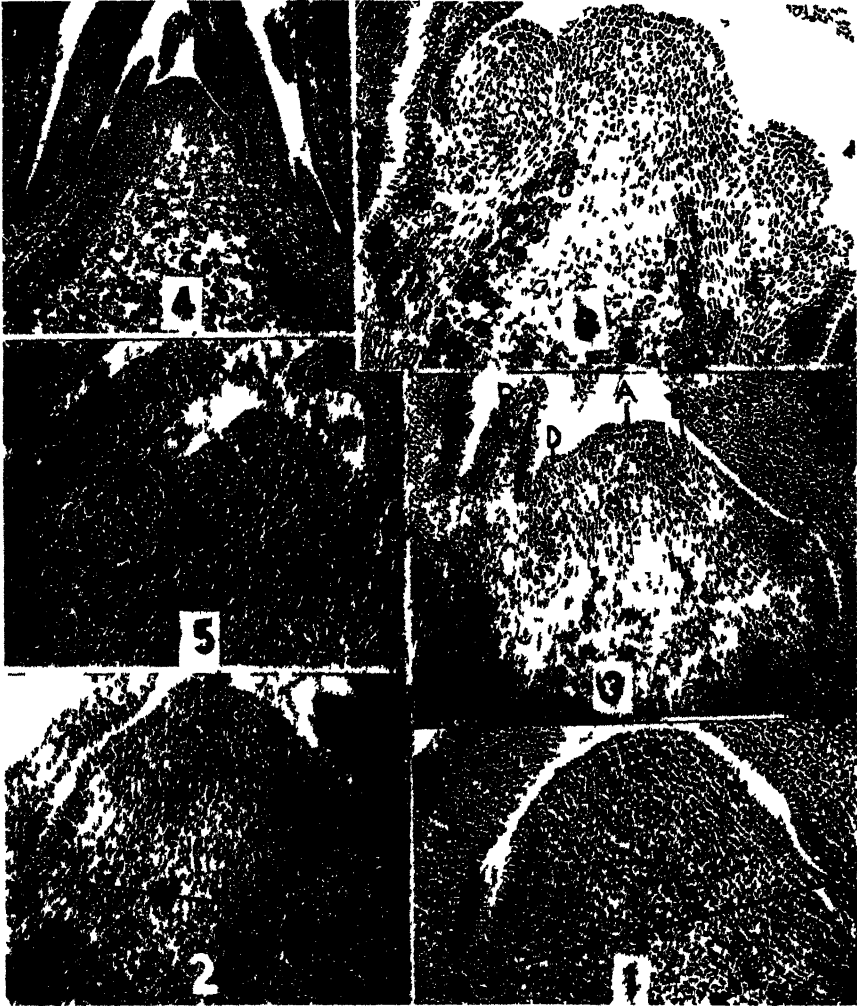
Fig. 2. A terminal (central) primordium and the beginnings of two lateral primordia of leaves or bracts.

Fig. 3. There are present a terminal primordium (A), the well developed primordium of a leaf or bract (B), the base of another well developed leaf or bract primordium (C), and two lateral primordia (D & E) of two more leaves or bracts just beginning to appear.

Fig. 4. The same bud showing a broadly conical provascular form.

Fig. 5. There are present two well developed primordia of bracts or leaves (A & B), a terminal (central) primordium (C), and two lateral primordia (D & E) of leaves or bracts just beginning to appear.

Fig. 6. There are present the primordium of a terminal blossom (the terminal primordium), and the two lateral primordia of two lateral blossoms. In each case the lateral primordium is in the axil of a bract.



AARON BUD DIFFERENTIATION

Anatomy of the spikelets and flowers of *Carex*, *Kobresia* and *Uncinia*

ROBERT S. SNELL

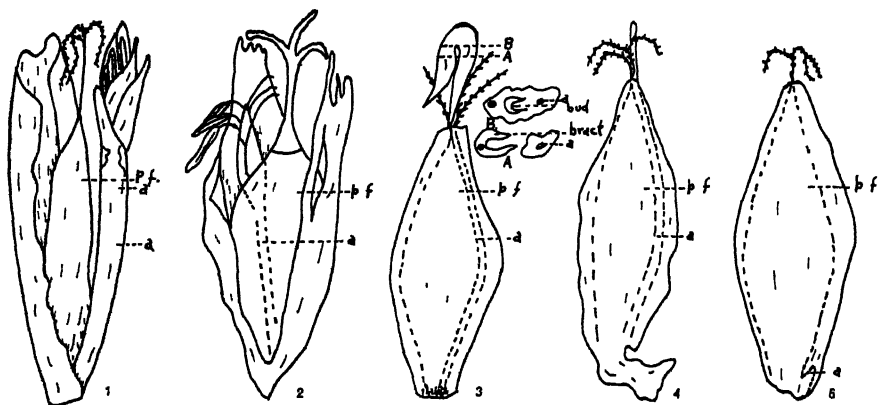
(WITH THIRTY TEXT-FIGURES)

Few problems have received more attention in the literature of plant morphology than has the attempted explanation of the pistillate "flower" of the sedge genus *Carex*. Most of the interest has centered about an interpretation of the morphology of the sac-like structure which immediately surrounds the pistil. (This structure is called the perigynium in American floras.) The status of the present knowledge of the pistillate "flower," with its perigynium, is given in the following pages, and the need for a thorough anatomical study of the "flower" is shown. Later pages give the result of such an anatomical investigation which has been carried on by the author for *Carex* and closely related genera, *Kobresia* and *Uncinia*.

Mackenzie (1931) places *Carex*, *Kobresia*, and *Uncinia* in the tribe Cariceae of the family Cyperaceae. The members of the tribe have unisexual flowers, and the achenes are enclosed in perigynia. Kükenthal (1909) placed *Carex*, *Kobresia* ("Cobresia"), *Uncinia*, and *Schoenoxiphium* (an African genus) in the group Caricoideae of the Cyperaceae. Staminate and pistillate flowers are produced in spikes of different order by the members of the group. Staminate flowers are borne on the axis of the spike; pistillate flowers are attached to short lateral axes of the spike, i.e., to spikelet axes. Pax (1889) placed *Carex*, *Kobresia*, *Uncinia*, and *Schoenoxiphium* in a group Caricoideae-Cariceae. Two other genera, *Elyna* and *Hemicarex*, were also included by Pax. Neither of these genera is recognized by Mackenzie or Kükenthal, but the members of the two are placed by these workers in either *Kobresia* or *Schoenoxiphium*. It will be seen that the Cariceae of Mackenzie, the Caricoideae of Kükenthal, and the prior Caricoideae-Cariceae of Pax represent the same group of sedges. The following are the group characteristics: unisexual flowers; a sac-like organ about the pistillate flower; staminate and pistillate flowers, for the most part, borne on axes of a different order.

The genera of the Cariceae, although they have the above characteristics in common, are distinct in many features, especially in the structure of the pistillate spikelet. In *Schoenoxiphium* (fig. 1) the axis of the pistillate spikelet is relatively large and well developed. At its base it bears a single pistillate flower, and usually, toward its tip, several staminate flowers. The pistillate flower, as in all members of the Cariceae, is a simple pistil. The pistil and the base of the axis are nearly enclosed by the perigynium

which in some species is open part way down the posterior side. In *Kobresia* (fig. 2) pistillate spikelets are similar to those of *Schoenoxiphium*, but the axis is not as conspicuous. In some species the axis of the spikelet bears no staminate flowers; in others staminate flowers are usually present. The perigynium is open or partly so, on the posterior side. In *Uncinia* (fig. 3) the axis of the pistillate spikelet is conspicuously exserted from the perigynium, and hooked at the end. The perigynium is completely closed. The axis of the pistillate spikelet of *Carex microglochin* (fig. 4) extends for some distance out of the orifice in the top of the perigynium. In several species of *Carex* (to be described later) the axis approaches the perigynium in length, but is entirely included. In most species the spikelet axis is abortive beyond the attachment of the pistil (fig. 5). In all species of *Carex* the perigynium is closed.



Figs. 1-5. Pistillate spikelets of *Schoenoxiphium*, *Kobresia*, *Uncinia*, *Carex microglochin*, and *Carex* sp., respectively. The perigynia of figures 1 and 2 have been pulled away to show spikelet axis *a* and the pistillate flower *p. f.*; both are shown by dotted lines in the other figures. (Figs. 1, 2, and 3 redrawn from Kükenthal.)

The pistillate spikelets of *Carex* were studied before those of *Kobresia* and *Uncinia*, but they were not recognized as spikelets at first since the spikelet structure is not evident in most of the species of the genus. In fact the interest early manifested in *Carex* centered about the perigynium. This structure is an unusual plant organ which does not lend itself readily to morphological interpretation. What fundamental organ or combination of organs does the perigynium represent?

In 1835 appeared Kunth's explanation of the perigynium and pistillate spikelet of *Carex* which, in the main, is accepted at the present time. Kunth was led to his explanation by a study of a species of *Schoenoxiphium*. According to Kunth the pistillate flower is reduced to a naked pistil borne

on the lateral axis of the spike. It arises in the axil of a large bract which is placed with its back to the main axis. This bract is bicarinate as a result of its position; it surrounds the pistil and lateral axis, and, by the fusion of its margins produces a sac-like covering. Kunth compares the perigynium with the upper palet of grasses, and the subtending bract of the pistillate spikelet of *Carex* with the lower palet of grasses. The perigynium of *Carex* and the upper palet of grasses are the first bracts of small lateral axes, and are called prophylls. The prophylls of a dicotyledonous plant are usually paired, opposite, and lateral. The single prophyll of a monocotyledonous plant lies between the lateral branch and the main axis with its back to the latter. Some dicotyledonous plants seem to have a single prophyll, and some monocotyledons seem to have paired prophylls like those normally found in dicotyledons (Arber, 1925). When there is a single prophyll, it is normally two keeled as a result of pressure against the axis; often there is a vascular strand in each keel. Gay (1838) first compared the perigynium of *Carex* with the prophylls which are found at the bases of the peduncles in many species of the genus; Roeper (1843) elaborated on the work of Gay. The theory that the perigynium represents a single bract with its back to the main axis (a prophyll), a theory founded on the views of Kunth, Gay, and Roeper, did not prevail at this early period, though at a later date it became the established theory.

In 1835 Nees ab Esenbeck regarded the perigynium as composed of two fused bracts, though it is not wholly clear from his geometrical representations what sort of bracts he had in mind. Lindley (1853), whose name became associated with the two-bract theory of the perigynium, groups *Carex*, *Uncinia*, and *Diplacrum* as genera of the Cyperaceae in which two opposite bracts are present. It is evident that Lindley compared the perigynium with non-homologous structures in *Diplacrum*. Robert Brown (1866) held with Lindley that the perigynium represents fused bracts. As with Lindley, Brown homologizes the perigynium with non-homologous structures in other genera (*Iris* and *Diplacrum*).

Payer (1857) introduced the ontogenetic attack on the problem of the perigynium. He concluded from a bud study of the developing perigynium that it is composed of two fused bracts. This conclusion was derived from the fact that the perigynium first appears in the bud as two opposite ridges, one on the right and the other on the left of the subtending bract. These ridges are joined as growth continues in a complete circumference, forming a sac-like perigynium.

It is interesting and significant that Payer worked with a species of *Carex* which possesses a strongly bidentate perigynium. In the ontogenetic development, two ridges appeared first as would be expected in a structure

which at maturity is strongly bidentate at the top. The top of the perigynium appears first, of course, in ontogeny. The teeth at the tip of a mature perigynium are represented at an early stage by two ridges. The rest of the perigynium, the sac-like portion below the teeth, is formed by growth in a continuous ring. In the light of the present knowledge of ontogenetic development generally, how can occurrences in this particular case be interpreted as indicating that the perigynium represents two fused bracts? Both Caruel (1867) and Schumann (1890) have shown that in another species of *Carex* the perigynium starts development as a ring of tissue.

The fact that many species of *Carex* possess rigidly bidentate perigynia and that the perigynia of many species are two-keeled with a strong vascular strand in each keel (these two vascular strands representing the entire supply to the perigynium) is seemingly the strongest evidence for the origin of the perigynium by the fusion of two bracts. Efforts of Lindley and Brown to substantiate the view with comparative morphological data and the effort of Payer to do the same with ontogenetic evidence have failed. Moreover, the bidentate condition of the perigynium seems to follow on its bicarinate nature which is, in turn, a result of the position of the perigynium, with its back against the spike axis. The morphological significance of the vascular strand in the keels is taken up on a later page. It can be said here that the general vascular condition in the perigynia of *Carex* and *Kobresia* does not support the theory that the perigynium arose phylogenetically by the fusion of two bracts.

Kunth's view that the perigynium represents a single bract, placed with its back to the main axis, which found backing and amplification in the work of Gay and Roeper who recognized the perigynium as a prophyll, has become the established view. Caruel (1867), Duval-Jouve (1864), Eichler (1875), Kükenthal (1909), Lotsy (1911), Pax (1885), Townsend (1873 and 1885), and others supported and advanced the theory that the perigynium of *Carex* is a prophyll. The theory that the perigynium represents two fused bracts has received slight support in the more recent literature on *Carex*. Some workers who have regarded the perigynium as a single bract have subscribed to the two-bract theory as an alternative explanation.

That the unit of the pistillate spike of *Carex* is not a flower in the true sense of the word but a spikelet was not realized by many of the early investigators. Interesting, at least, and perhaps significant is the fact that most of those who backed the theory that the perigynium represents fused bracts make no mention of the abortive axis of the spikelet, nor do they indicate that the unit structure in the pistillate spike of *Carex* is a spikelet

and not a flower. Payer refers to the pistillate spikelet as a flower. Lindley says "their flowers" when obviously he means the pistillate spikelets of *Carex*. Kunth and proponents of his theory have generally realized that the pistillate flower of *Carex* consists of a naked pistil only, and that it is the subtending bract of the pistillate flower which forms the perigynium. Later workers recognized it as a prophyll. Their evidence for such an interpretation came largely from comparative morphology; the spikelets of *Kobresia*, *Uncinia*, and *Schoenoxiphium* were used in arriving at a satisfactory explanation of the more obscure pistillate spikelet of *Carex*. The presence of a minute remnant of a phylogenetically aborted axis within perigynia of young spikelets of *Carex* confirmed what comparative morphology strongly indicated.

To Kunth belongs the credit of proposing at an early date (1835) an explanation of the perigynium and spikelet of *Carex* that harmonizes with all later found important evidence, and remains today essentially unchallenged.

As stated in the introduction, it was in part for the purpose of ascertaining, by a thorough anatomical analysis, the actual morphology of the pistillate spikelets, of *Carex* especially, and also of *Kobresia* and *Uncinia* that this investigation was started. An attempt has been made also, by a study of the vascular supply, to arrive at the structure of the ovary and ovule of the *Carex* flower.

METHODS

Spikelets for study were, in all cases where possible, cut singly from the axis of the spike with specially ground fine-tipped scissors. A small portion of the spike axis where the axis of the spikelet joins it was detached with each specimen. In the case of those species of *Carex* having a very dense spike, a portion of this was taken as a specimen, a procedure employed also with staminate spikes.

Butyl alcohol was used in dehydration and the material was imbedded in hard paraffin. Vascular development in the spikelets is practically complete at flowering time. By taking the spikelets at this early stage or soon after, using butyl alcohol as a dehydrating agent, and employing a hard paraffin, sufficiently thin serial sections could be cut with a rotary microtome. It is, however, impossible to cut spikelets in late fruiting stages by this method. Herbarium material was soaked in warm water or weak alkali solutions as a preliminary treatment.

All of the cross and longitudinal sections employed in this investigation were cut serially, as outlined, in a rotary microtome. All figures of such sections have been drawn directly without the use of camera lucida

or projection apparatus; hence figures represent magnifications of various degrees. Specimens of a given species from different parts of a plant, from different plants, from plants in different places, from plants of more than one season were employed to avoid possible individual abnormalities. Three specimens, at least, were consulted in arriving at any general conclusions on a particular species. It will be seen that most of the species of *Carex* employed are from the northeastern part of the United States. Material of morphologically important species, and of other genera not found in this region, was obtained from herbarium specimens.

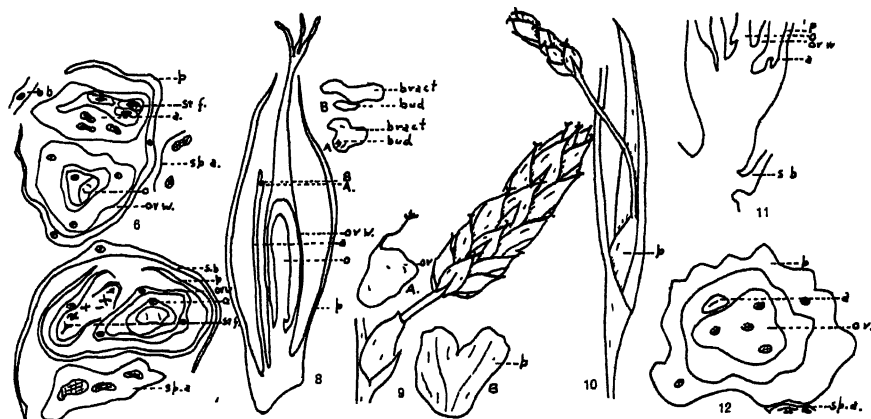
ANATOMY OF THE PISTILLATE SPIKELETS

Because a detailed knowledge of the pistillate or bisexual spikelets of *Kobresia*, of certain abnormal *Carex* spikelets, and of the pistillate spikelets of *Uncinia* may be of help in understanding the more obscure spikelet condition normally found in *Carex*, these forms are treated first. The bisexual spikelet is found normally in close living relatives of *Carex*, but only in abnormal forms of the genus *Carex* itself. *Kobresia* offers a good example of the probable primitive *Carex* spikelet. The spikelet axis of *Kobresia* does not abort beyond the place of attachment of the pistillate flower, but becomes nearly as long as, or in some cases even longer than the perigynium. In its terminal portion it usually produces one or more staminate flowers with their bracts (figs. 2 and 7). A bisexual spikelet, corresponding to that usually found in *Kobresia* is found abnormally in some species of *Carex*. Normally in *Carex filifolia* the axis of the spikelet is a flat structure of medium length which lies against the achene. But some spikelets of *C. filifolia* which were encountered accidentally, in material which had been taken for sectioning, showed a strictly bisexual state like that in *Kobresia*. In these spikelets the axis is very well developed, and produces two or three staminate flowers near its tip (fig. 6). Within this species such abnormalities are not in any sense common, so far as could be determined, for in the limited amount of material at hand it was impossible by searching to find more of these abnormal spikelets. *Carex eburnea* afforded a less striking abnormality of the type just described in *C. filifolia*. Usually, in this species, it is the axis of the spikelet which is abortive; the ovary, well developed and fertile. In one abnormal spikelet which was sectioned the ovary was abortive; and the axis, a fairly well developed one, produced three abortive stamens. Apparently the axis developed at the expense of the ovary.

There is no fossil evidence to establish a primitive bisexual spikelet in the genus *Carex*. The evidence of comparative morphology favors such a primitive spikelet in *Carex*. Thus the abnormal bisexual spikelets of *C.*

filifolia may be reversionary. The abnormality in *C. eburnea* suggests a primitive bisexual spikelet in the genus.

A group of near relatives of *Carex* are set off by themselves, among other things, by a peculiar hook-like spikelet axis (fig. 3). This group is the genus *Uncinia*. Actually, the end of the axis is more than just a hook, as a microscopic examination of serial sections of that region shows. The hooked tip is a bract rolled in from the sides and sharply pointed. A cross section of the axis at the level A (fig. 3A) shows the inrolled bract clearly.



Figs. 6 and 7. Cross sections of an abnormal bisexual spikelet of *Carex filifolia* and a normal bisexual spikelet of *Kobresia caricina*, respectively, to show the similarities.

Fig. 8. Median longitudinal section of the normal pistillate spike of *Carex capitata*. Sections of the spikelet axis at two levels near the tip are shown.

Figs. 9 and 10. Anomalous spikelets of *Carex Schweinitzii* and *C. paupercula*, respectively. The basal prophyll B and its contained ovary A of *Carex Schweinitzii* are shown.

Figs. 11 and 12. Median longitudinal and cross sections, respectively, of the base of a pistillate spikelet of *Carex Woodii*.

a, spikelet axis; o, ovule; ov. w., ovary wall; p., perigynium; s. b., subtending bract of spikelet; sp. a., spike axis; st. f., staminate flower.

A similar section at the level B (fig. 3B) shows a bud which the bract subtends. No specimens of *Uncinia* examined (two or three species were available) showed any further development of the bud. However, the report by Benthams (1873) of finding an anther attached to an abnormal seta (axis of the spikelet) of *Uncinia* may mean that the bud which is normally abortive did, in one case, develop (perhaps a reversionary phenomenon) sufficiently to produce at least one stamen. If this surmise is correct, we have another bit of fragile evidence for an ancestral bisexual spikelet for the genus *Uncinia*; hence, evidence for a primitive bisexual spikelet in the closely related genus *Carex*. Certainly there is a prevalence

of bisexual spikelets normal and abnormal, in the genus *Carex* and its near relatives.

Nearly every species of *Carex* shows some remnant of the spikelet axis within the perigynium at flowering time and even later. Usually it is no more than a small knob of tissue with no indication of component organs, such as bracts or a terminal bud (figs. 11 and 12). A few species of *Carex* possess spikelets with long axes, long enough in one case (*C. microglochin*) to extend, along with the stigmas of the pistil, out of the orifice of the perigynium (fig. 4). There is no hook at the end as in the genus *Uncinia*. In *C. capitata* the axis, though shorter than in *C. microglochin* so that it is included within the perigynium, is more significant from the standpoint of the morphology of the spikelet. A close inspection of the top of the axis under a dissecting microscope discloses a terminal bud with its subtending bract. A median longitudinal section of the spikelet shows the same thing even more clearly (fig. 8).

Rather frequently one finds pistillate spikelets of *Carex* in which the, in one sense, spikelet axis develops abnormally to the extent of becoming a spike axis. Usually this excessive development of the axis takes place at the expense of the ovary which does not show at all, or, if present, is distorted and sterile. Material of *C. paupercula* contained a not infrequent abnormality (fig. 10). In this particular specimen the perigynium bore no ovary in its axil. An abnormality of *C. Schweinitzii* is pictured in figure 9. The prophyll at the base of the axis does not look much like a perigynium, but a much distorted ovary was found in its axil. Numerous cases of proliferating spikelets have been reported in the literature of *Carex*: Borner (1913), Duval-Jouve (1864), Hegelmaier (1887), Holm (1896), Reichardt (1861), Ridley (1884), Schulz (1887), Schumann (1890), Thiselton-Dyer (1875), Townsend (1885), Urban (1880), and Wesmael (1863). A good comprehensive account of anomalous spikelets of *Carex* may be had in "Pflanzen-Pathologie und Pflanzen-Teratologie" by Moquin-Tandon (1842).

These anomalous conditions can not hastily be interpreted as reactionary. They occur in species where the axis of the spikelet is normally reduced to a mere vestige. There are proliferations, grotesque aberrations, that can be expected to tell little or nothing about the detailed structure of the primitive spikelets of *Carex*. They do tell, however, that one is dealing with a spikelet in *Carex*, and that the normally abortive axis of the spikelet under certain conditions is capable of prolonged growth. It may possibly be that some of these anomalous cases are not proliferating spikelets at all, but merely normal spikes developing from a basal prophyll. All of the species of *Carex* in which there are separate staminate and pis-

tillate spikes have prophylls at the bases of the peduncles. These normally are not fertile, i.e., they do not bear pistillate flowers in their axils, but they may under abnormal conditions do so. Prophylls at the bases of the lower peduncles of the inflorescence are usually sheath-like and hyaline, entirely covered by the sheaths of the leaves subtending the lateral axes on which the prophylls are borne, but the prophylls of the upper peduncles are often partially exposed to the elements because subtending leaves in this region are short and bract-like with small or no leaf sheaths. In general the upper prophylls are heavier in texture and have more the appearance of perigynia than do the lower. Anomalous growths of the types that have been described may represent proliferated spikelets or they may represent normal spikes that grow from abnormal prophylls. Perhaps such growths are of two distinct kinds. Perhaps, in a general way, those in which the prophyll subtends a pistil represent abnormally developed spikelets, while those in which the prophyll subtends no pistil are true spikes with perigynium-like prophylls. The present knowledge of abnormalities is so meager that there is no basis for a convincing interpretation of them. That these shoots are reversionary, of course, can not be denied as a possibility. From the normal spikelets of *Kobresia* and *Schoenoxiphium*, and from occasional abnormal spikelets of forms like *Carex filifolia*, the evidence is strong that the ancestral spikelet of *Carex* was bisexual, staminate at the apex and pistillate at the base. It is quite possible, too, that reduction, in some cases at least, has occurred from spikelets which were pistillate in their extremities. The same type of spikelet may not be ancestral to the pistillate spikelets of all present day species of *Carex*.

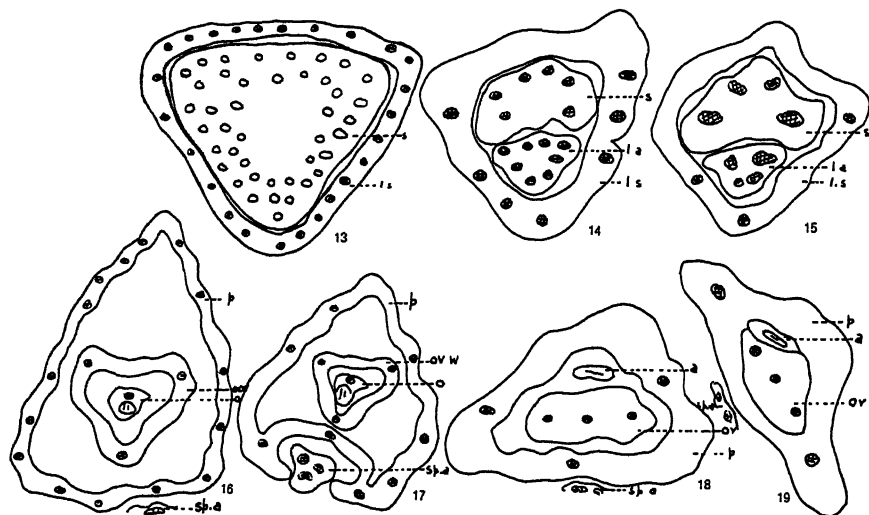
ANATOMY OF THE PERIGYNIMUM

In literature dealing with *Carex* it is around a morphological interpretation of the perigynium that early controversy developed. Does it represent one or two bracts? Is it simply an especially modified prophyll? It was with real interest that serial sections of spikelets of *Carex* were examined to get the evidence which the number, position, and course of vascular strands affords.

Because of the resemblance in the position and accompanying bicarinate condition of perigynia and pedunculate prophylls of *Carex*, an anatomical comparison of the two was attempted. It was found, however, that the pedunculate prophylls are usually entirely without vascular strands, a fact to be correlated with their delicate hyaline nature. This, in turn, is the result of their being entirely enclosed by the leaf sheath which subtends the axis to which the prophyll is attached.

Because it was observed that the prophylls of *Zebrina pendula* are

simply leaf sheaths (fig. 20) a gross comparison of leaf sheaths and pedunculate prophylls of several species of *Carex* was made to determine whether or not the same relation holds in this genus. The similarity of form (figs. 23 and 24), identical relations of chlorenchymatous and hyaline areas in leaf sheath and upper prophyll of some species (figs. 21 and 22), and identical markings in subtending bract and upper prophyll of *Carex communis* (figs. 25 and 26) led to the conviction that the prophyll of



Figs. 13-15. Cross sections of leaf sheaths of *Carex intumescens*, *C. platyphylla*, and *C. pedunculata*, respectively.

Figs. 16-19. Cross sections of perigynia of *C. intumescens*, *C. platyphylla*, *C. aurea* (abnormal), and *C. cristata*, respectively.

a, spikelet axis; *l. a.*, lateral axis; *l. s.*, leaf sheath; *o.*, ovule; *ov.*, ovary; *ov. w.*, ovary wall; *p.*, perigynium; *s.*, stem; *sp. a.*, spike axis.

Carex is usually the sheath of the first leaf of a lateral axis. It is normally bicarinate and hyaline because of its position and environment, respectively. A comparison of the vascular supply to the perigynia with that to leaf sheaths immediately suggested itself. A series of cross sections of leaf sheaths of various species of *Carex* is shown in figures 13-15. In the lower leaf sheaths of *C. intumescens* the vascular strands are numerous and distributed through a complete circumference. It will be noted that the strands are not so prominent in the thin portion of the leaf sheath opposite the midrib. Leaf sheaths of *Carex platyphylla* and *C. pedunculata* show fewer strands, all limited to that portion of the leaf sheath under the leaf blade.

An examination of the cross section of the perigynium of *C. intumescens* (fig. 16) shows a distribution of vascular strands like that in a lower leaf sheath. In *C. platyphylla* the distribution of strands in the cross section of a perigynium (fig. 17) is very much like that in a leaf sheath of the same plant. One perigynium of *C. aurea* (fig. 18) shows three vascular strands distributed like those in a leaf sheath of *C. pedunculata*. Usually in this species there are but two vascular strands running in or near the keels, as in the figured perigynium of *C. cristata* (fig. 19). The fact that, as in *C. cristata*, the perigynia of many species of *Carex* are bicarinate with a single prominent vascular strand in each keel has always been a strong argument for the origin of the perigynium of *Carex* by the fusion of two bracts. That occasionally, as in *C. aurea*, a third strand is present in the middle of the perigynium, which normally has but a strand in each keel, indicates that the perigynium of the species earlier (phylogenetically) had a midrib which has aborted. Abortion of a strand has occurred in that part of the perigynium which is crowded against the spike axis. Successive cross sections from the base of a pistillate spikelet of *C. digitalis* show abortive strands in this same region. A section near the base of the spikelet shows two strands toward the spike axis (fig. 27). A section just above shows them completely absent (fig. 28).

The vascular strands often found in the keels of a perigynium are not midrib strands of fused bracts, but they represent lateral strands of a single bract. These strands remain in regions of tissue prominence, the keels, after abortion of a midrib strand or middle strands in a region where growth is stunted by pressure of the perigynium against the axis of the spike. In the perigynia of *Carex* a reduction series exists from the many-stranded perigynia of species like *C. intumescens* and *C. platyphylla* to the two-stranded perigynia of species like *C. cristata* and the normal *C. aurea*.

The fact that the perigynium represents a single bract is further shown by its position in relation to the pistil. In the sedge family (Cyperaceae) one angle of the tricarpellate ovary (in species possessing such) is opposite the subtending bract of the flower. In those genera in which the spikes are simple, the subtending bract is attached directly to the axis of the spike (fig. 29). In species of *Carex* one angle of a tricarpellate pistil is turned toward the middle region of the perigynium, a prophyll, hence to that portion which lies against the spike axis. In other words, the orientation of the tricarpellate pistil of other genera of sedges to the subtending bract of the flower is the same as that found in tricarpellate species of *Carex*. In recognizing the perigynium as the subtending bract of the pistillate flower of *Carex*, any seeming incongruity in the position of the pistil among various genera of the Cyperaceae vanishes.

In those species of *Carex* in which the vascular strands of the perigynium are fairly numerous the midrib of the perigynium lies opposite an angle of the tricarpellate pistil (figs. 16 and 17). The fact that in some species of *Carex* there is a midrib in the perigynium opposite an angle of the tricarpellate ovary, supports the view that the perigynium represents a single bract. Such a position is entirely incompatible with the theory

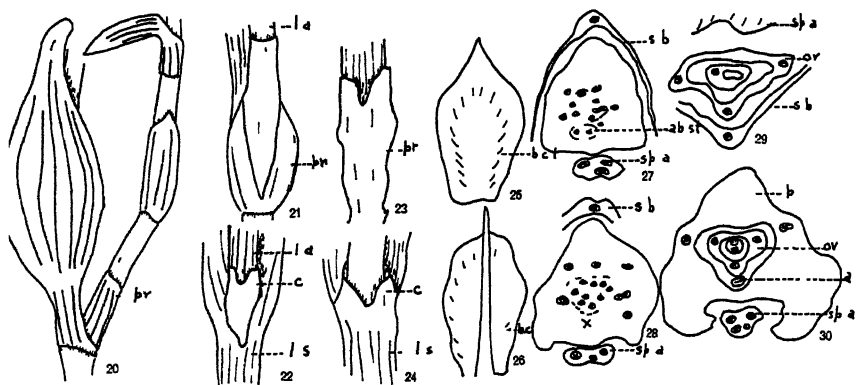


Fig. 20. Prophyll and adjacent parts of *Zebrina pendula*.

Figs. 21 and 22. Upper pedunculate prophyll and leaf sheath, respectively, of *Carex platyphylla*.

Figs. 23 and 24. Pedunculate prophyll and leaf sheath, resp., of *Carex laxiflora*.

Figs. 25 and 26. Uppermost pedunculate prophyll and opposing leaf sheath, resp., of *Carex communis*.

Figs. 27 and 28. Successive sections from the base of a pistillate spikelet of *Carex digitalis* to show abortive perigynial vascular strands.

Fig. 29. Diagram to show position of pistil in relation to subtending bract of flower in *Scirpus* sp.

Fig. 30. Cross section of base of reflexed pistillate spikelet of *Carex microglochin*.

a, spikelet axis; *ab. st.*, abortive perigynial vascular strands; *b. c. l.*, brownish color line; *c.*, hyaline collar-like projection of leaf sheath; *l. a.*, lateral axis, *l. s.*, leaf sheath; *ov.*, ovary; *p.*, perigynium; *pr.*, prophyll; *s. b.*, subtending bract of pistillate spikelet or flower; *sp. a.*, spike axis.

that the perigynium represents two fused bracts. Even where a midrib is lacking, the angle of the ovary is directed toward the middle part of the perigynium which indicates that the absence of a midrib is a matter of phylogenetic abortion, an abortion correlated with its unfavorable position. A strand or strands have been lost where the development of surrounding tissues is least.

The results of an anatomical study of the perigynium clearly substantiate the view which Kunth held of the morphological nature of the perigynium. It is a single bract. It is a prophyll by position and by its bicari-

nate nature. A prophyll is the first leaf of a lateral axis; in *Carex* usually the leaf sheath only is present. When there are many vascular strands in the perigynium they show a distribution similar to that found in a leaf sheath of *Carex*. The perigynium sheaths the axis on which it is borne like a leaf sheath. Both its vascular supply and its gross morphology are that of a leaf sheath.

Because the perigynium is often bicarinate with a vascular strand in either keel (fig. 19) early workers on *Carex* thought that the perigynium represents two fused bracts and that the two strands represent midrib bundles of the bracts. In the absence of conflicting evidence these relations within the perigynium might be accepted as hinting that the perigynium has arisen in this way. But, in general, the course of vascular strands does not indicate derivation of the perigynium from two fused bracts. In many cases the vascular strands do not run in the keels of the perigynium though their course is in harmony with the position of the keels. Often the vascular strands do not even conform in their course to the keels. The explanation of this divergence seems to lie in the following facts. The keels result ontogenetically from the pressure of the perigynium against the axis of the spike. The vascular supply phylogenetically became adapted through reduction to the keeled state. Pressure disturbances or aberrations in the development of a particular spikelet would account for nonconformity between the keels of a perigynium and the course of vascular strands in the perigynium. A recent phylogenetic change in the spike habit of a particular species might account for a normal discrepancy between keels and the course of vascular strands in the perigynia of that species. Especially illuminating in this respect is the relation between the position of keels and vascular strands in spikelets of *C. microglochin*. In this species the spikelets early turn back on the parent axis (reflexed spikelets) so that the opposite side of the perigynium is appressed to the spike axis. In the cross section of the base of a spikelet (fig. 30) it will be seen that under this condition the keels are on the side of the spikelet opposite that on which they are in other species. In *C. microglochin* they are on the same side of the spikelet axis; in other species they are not.

Not only is the two-bract theory of the perigynium refuted by the anatomical evidence from perigynia with many strands, but it is not supported in perigynia with two strands. Sometimes keels are not even present. The keels are often not traversed by the vascular strands. The only possible support for the two-bract theory lies in the possibility that, though the keels can not be interpreted as midribs of bracts, the two vascular strands present in many perigynia represent midrib strands. There is evidence against this possibility. In occasional perigynia bearing but

a single vascular strand no other deviations from the normal are noted. If the strands actually represent the midribs of two fused bracts, one might expect to find the absence of the vascular strand accompanied by the lack of its bract, and hence, some serious malformation of the perigynium.

As has been stated in defense of the one-bract theory of the origin of the perigynium, the bicarinate nature of the perigynium is a result of its position. Pedunculate prophylls of *Carex* are bicarinate, yet these prophylls are simply leaf sheaths. Prophylls of monocotyledons, generally, are typically bicarinate but there are none which are known to have arisen by the fusion of bracts. Why the first leaf of a lateral branch of a monocotyledon should occupy the position it does against the main axis, is not known, but occupying that position, one can readily understand how pressures in the bud and in later development could make it bicarinate.

The bidentate tips of perigynia of many species of *Carex* can be correlated with the bicarinate nature of the perigynia possessing them, and should not be used as evidence for the origin of the perigynium in the fusion of two bracts. With greater development of vascular and non-vascular tissues in the keels, one can expect a tendency toward a greater terminal development of the keel regions than of the regions between. Such development has occurred in perigynia that have bidentate tips. Many perigynia terminate in an even ring of tissue.

This writer feels that the two-bract theory of the perigynium never would have had support if all the different types of perigynia had been examined. It is only the extremely reduced perigynia with prominent keels and accompanying vascular strands which even suggest the origin of the perigynium by the fusion of bracts.

In only one tricarpellate species of *Carex* was there found a significant deviation from the normal relation in position between one carpel and the middle portion of the perigynium. In *Carex pubescens* one angle of the ovary, instead of being directed toward the middle region of the perigynium, lies toward one or the other of the two perigynial strands. This orientation is fundamental; the lateral strand behaves in every respect of departure, gap formation, and orientation to flower as does the midrib of perigynia that possess such a strand. This orientation is not represented by a single abnormality, but is characteristic of the species. This peculiarity can hardly be regarded as evidence for the origin of the perigynium of *C. pubescens* in the fusion of two nearly opposite bracts. This species is but one of about fifty tricarpellate species that were investigated anatomically. The very abundance of opposing evidence moves one to regard the spikelet of *C. pubescens* as not representing a primitive condition for

the position of the pistil in relation to the perigynium. Probably the unusual orientation of pistil to perigynium in this species is of recent origin. The perigynium is of the reduced type with two lateral well developed vascular strands. It is possible, at least, that there has been a reorientation of the pistil because of the presence of the large lateral vascular strands and the absence of a midrib in the perigynium.

Probably both perigynia and prophylls of the peduncles of *Carex* have been derived phylogenetically from leaf sheaths. (There is evidence that the blade may sometimes be involved.) The trend of modification has been directed differently in the two cases. In the case of the pedunculate prophylls the trend has been toward extreme reduction and apparently toward disuse. It is difficult to ascribe any function to the hyaline slender prophylls of the peduncles. On the other hand, perigynia represent leaf sheath modification in the direction of structural and functional amplification. Perigynia are always inflated structures, often bidentate at the top, sometimes very large and richly supplied with vascular tissue. The perigynium always surrounds the ovary; and because of its early development and maturity, by comparison with the ovary itself, must offer to the latter a certain protection against water loss and mechanical injury by insects and other small animals. The perigynium protects the developing ovary in the absence of any floral protective parts. Undoubtedly perigynia aid in dissemination of the fruits of *Carex* by giving added buoyancy for transportation by water. Perigynia of various species of *Carex* can be found in some quantity on back water and pool surfaces. Even the difficulty that was experienced in exhausting air bubbles from mature and dry perigynia, in treating them preparatory to infiltration, is convincing evidence that they represent efficient floats. The distribution of various species of *Carex* along stream beds indicates the practical efficiency of the perigynia in this way.

THE PISTILLATE FLOWER OF CAREX

Usually the pistillate flower of *Carex* is made up of three or two fused carpels though in one subgroup, *C. concinnoides* of Mackenzie, the pistil is normally composed of four fused carpels (St. John and Parker, 1925). Ovaries of the tricarpellate pistils are normally more or less triangular in cross section, whereas bicarpellate ovaries are elliptical. The ovary is always unilocular with a single, basal, anatropous ovule whose stalk is toward the axis of the spikelet.

The gross morphology of the pistillate flowers of *Carex* has long been known, but practically nothing has been written about the internal anatomy, especially the vascular structure. Yet it is the nature of the vascular

supply within the pistillate flower which may furnish the key to a proper interpretation of the phylogenetic development of the flower. Though the number of stigmas and the lobing of the ovary suggests that the pistils of *Carex* are normally either bicarpellate or tricarpetate, they should be studied anatomically to see whether the vascular supply will suggest another interpretation. The presence of a single basal ovule in a unilocular bicarpellate or tricarpetate pistil represents, according to the criteria of comparative floral morphology, an extremely reduced pistillate condition. An anatomical study of the vascular supply to the basal ovule of *Carex* should enable one to determine the type of ovule placentation from which the basal ovule, by reduction, has been derived. Perhaps it can be determined what the relation is between tricarpetate and bicarpellate pistils. Is there any vestigial vascular structure at the base of the bicarpellate pistil which would indicate its origin by reduction from the tricarpetate type of pistil?

An anatomical study of the pistillate flowers of *Carex* has been made. For the most part, the vascular supply of ovary and ovule has been involved; to a limited extent, the supply of the receptacle and of the stigmas. The vascular supply to the ovary wall and ovule has been interpreted in terms of dorsal strands (midrib strands of the component carpels) and ventral strands (marginal strands of the carpels, which normally represent the placental vascular supply). In many species of *Carex* the vascular supply of the receptacle is so confused by anastomoses of strands that one can not interpret it except in its gross features. In other species, however, the vascular supply to the parts of the simple flower can be interpreted in terms of dorsal and ventral carpel strands arising in the receptacle of the flower.

In tricarpetate pistils, for these are evidently more primitive than bicarpellate ones and hence deserve consideration first, the dorsal strands of the carpels run in the angles of the ovaries and up into the stigmas. The ventral bundles of the three carpels are never distinct, but are represented usually by three strands. These, which probably before an early (phylogenetic) fusion were six (three pairs), fuse in the receptacle of the flower to form the single ovular strand. The fact that the entire ventral supply of all the carpels making up the pistil enters the single basal ovule indicates that the immediate ancestral type of placentation for *Carex* was free central.

Baillon (1893), after ontogenetic studies, says of some bicarpellate and of some slightly abnormal tricarpetate pistils of *Carex* that what shows first of the female flower is a small hemispherical receptacle on the surface of which develop a little later two or three carpels of which one is anterior,

and that it is this latter which often remains smaller than the others and finally entirely disappears. Schumann (1890) writes of a similar condition in *Scirpus*. There is scant anatomical evidence for phylogenetic abortion of the anterior carpel. Abortive vascular tissue is found in the position which the anterior carpel would occupy if present. The detailed vascular structure of this abortive carpel is not discernible in any specimens that have been examined. (In general the vascular supply of bicarpellate pistils examined was more limited in amount and more involved than that of tricarpellate pistils.) What little anatomical evidence there is for the origin of the bicarpellate pistil harmonizes with the results of the ontogenetic bud studies of Baillon and Schumann.

SUMMARY

1. Anatomical evidence for the morphological nature of the pistillate "flower" of *Carex* substantiates previous findings of comparative morphology and of ontogenetic studies. The pistillate "flower" of *Carex* is a spikelet bearing a single, naked, pistillate flower. The axis of the spikelet is usually abortive beyond the attachment of the pistil.

2. Primitively the spikelet was probably bisexual as it is in present day species of close relatives of *Carex*, i.e., *Kobresia* and *Schoenoxiphium*. The author has found and figured abnormal bisexual spikelets of *Carex*.

3. Normally the naked pistillate flower of the spikelet is surrounded and hidden, with the exception of the stigmas, by its subtending bract, the perigynium. The spikelet axis from the attachment of the perigynium outward is also included within the perigynium.

4. The perigynium represents a single bract, as first stated by Kunth. It is a prophyll as determined by Gay.

5. Although having certain characteristic features such as a bicarinate form, often with a vascular strand in each keel, a prophyll is the first leaf of a lateral axis. Usually only the sheath of this leaf is present in *Carex*, as in *Zebrina pendula*.

6. The perigynium thus usually represents the sheath of the first leaf of a lateral axis. The fact that it is a leaf sheath, readily accounts for the way in which it includes the axillary pistillate flower and the end of the axis.

7. Statement 6 of this summary is substantiated by the fact that the vascular supply of perigynia with many strands is like that of leaf sheaths of *Carex*. A reductional series from many-stranded perigynia to those with only two strands exists, showing that the latter represent the product of a phylogenetic vascular modification.

8. Excellent confirmatory evidence for the statements of sections 3, 4, and 5 of this summary is seen in the position of a tricarpellate pistil of

Carex in relation to the perigynium. One angle of the ovary lies opposite the midrib of the perigynium if a midrib is present, and always, with one exception noted by the author, opposite the middle region of the perigynium. This corresponds to the condition in other genera of the Cyperaceae, where one angle of the ovary lies opposite the midrib of the subtending bract of the flower.

9. In the compound pistils of *Carex*, *Uncinia*, and *Kobresia*, and presumably in all the genera of the Cyperaceae, the dorsal bundles, that is, the midribs of the carpels, run unbranched through the ovary to enter the stigmas. In most cases the ventral bundles of a carpel do not exist separately but as a single bundle, because of phylogenetically earlier fusion; rarely they may be separate. The two or three ventral fusion bundles all fuse together in the receptacle of the flower to form the vascular strand which runs into the single, basal, anatropous ovule.

10. The ovule is always single, basal, and anatropous. Because of its constant singleness and basal position and because of the nature of its vascular supply (outlined in section 9 of this summary), it seems certain that the ovule represents the limit of reduction from several ovules and free central placentation.

11. Although anatomical evidence for the phylogenetic abortion of the anterior carpel of a tricarpellate pistil to form the bicarpellate pistil of many species of *Carex* is meager, it does confirm the positive ontogenetic evidence of Payer and Schumann.

The writer wishes to express his gratitude to Professor Arthur J. Eames of Cornell University for suggesting this problem, and for his advice and criticism during the investigation.

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Studies of South American plants—V
Additional notes on Thibaudieae

ALBERT C. SMITH
(WITH THIRTEEN FIGURES)

CERATOSTEMA Juss. Gen. Pl. 163. 1789

(*Englerodoxa* Hoer. Bot. Jahrb. Engler 42: 310. 1909)

In preparing my monograph of Thibaudieae¹ I did not have access to the type of the genus *Ceratostema* (*C. peruvianum* Gmel.). Since that time, however, I have seen that specimen in the herbarium of the Museum d'Histoire Naturelle, Paris (herb. Jussieu 7579), and have come to the conclusion that it is congeneric with *Englerodoxa*. This conclusion was independently reached by Dr. Sleumer, who has recently² published his findings. *C. peruvianum*, although reported from "Peru," was probably originally collected within the present limits of Ecuador, where it has since been found by Sodiro. *Ceratostema* is represented by the five species listed below, all of which appear to be limited to Ecuador. The genus belongs in the group of genera related to *Siphonandra* and is characterized by long angled corollas swollen at the base, elongate corolla lobes, and long tubules dehiscing by oblique pores. My previous notes on *Englerodoxa* may be taken to apply to *Ceratostema*.

CERATOSTEMA ALATUM (Hoer.) Sleumer, Notizbl. 12: 281. 1935.

Englerodoxa alata Hoer. Bot. Jahrb. Engler 42: 311. 1909.

CERATOSTEMA PERUVIANUM Gmel. Syst. Nat. 2: 676. 1791.

CERATOSTEMA LORANTHIFLORUM Benth. Pl. Hartw. 142. 1844.

Ceratostema chillacochense Danguy & Cherm. Bull. Mus. Hist. Nat. Par. 28: 435. 1922.

Englerodoxa loranthiflora A. C. Smith, Contr. U. S. Nat. Herb. 28: 352. 1932.

I have recently seen the type of *C. chillacochense* (Ecuador: Rivet 772, herb. Paris), which is undistinguishable from *C. loranthiflorum*.

CERATOSTEMA CALYCINUM Benth. & Hook. f. Gen. Pl. 2: 570. 1876, nomen.

Anthropterus calycinus Spruce, Pl. exs. n. 5094, nomen.

Englerodoxa calycina A. C. Smith, Contr. U. S. Nat. Herb. 28: 351. 1932.

¹ Smith, Albert C. 1932. The American species of Thibaudieae. Contr. U. S. Nat. Herb. 28, part 2: 311-547. pl. 1-19.

² Notizbl. 12: 279. 1935.

CERATOSTEMA ALBERTI-SMITHII (Sleumer) Sleumer, Notizbl. 12: 282. 1935.

Englerodoxa Alberti-Smithii Sleumer, Notizbl. 12: 57. 1934.

In view of the above disposition of the type species of *Ceratostema*, it is obvious that the 16 species which in my monograph were placed in that genus must be elsewhere referred. There having been no other available generic name, Dr. Sleumer has placed these species in his new genus *Pellegrinia*.

In my discussion of "*Ceratostema*" (loc. cit., p. 327-329) it was stressed that three distinct species groups are apparent. These groups differ from one another to such an extent that their close alliance is seriously to be doubted. I would have been inclined to recognize three genera for these species, had it not been for the difficulty of placing *Ceratostema peruvianum*. My studies since 1932 have strengthened my belief that this group is not natural, and the discovered congeneracy of *Ceratostema peruvianum* with *Englerodoxa* clarifies the situation.

In *Pellegrinia*, we have a group of four species which is characterized by continuous calyces, by anthers with slender tubules with small terminal or oblique pores, and by retrorsely pilose filaments. The anther characters are distinctly those of the genera allied to *Siphonandra*. The filaments conspicuously bear a dorsal mass of short retrorse hairs, a character not found elsewhere among the American Thibaudieae. If the genus *Pellegrinia* is to be divided, as I propose, this group must retain Dr. Sleumer's generic name. Geographically it appears to be limited to the Andes of Peru.

The remaining species of "*Pellegrinia*" have anthers with comparatively broad and flexible tubules which dehisce by elongate clefts. Such anthers are found among the relatives of *Thibaudia*, which is doubtless a close ally of these species of "*Pellegrinia*." These species fall into two groups, with clearly defined geographic limits. The first group, occurring from central Peru to northern Bolivia, will be known as *Demosthenesia*. It differs from *Pellegrinia* by its slightly dimorphic stamens, broad tubules with elongate clefts, and the sparse spreading hairs of the filaments. In superficial appearance, and in habitual features such as the frequent presence of aristate stipules, the species of *Demosthenesia* closely resemble those of *Pellegrinia*, but the common characters of the two groups appear to have arisen from different ancestries. While *Pellegrinia* doubtless belongs among those smaller genera with highly specialized stamens, such as *Siphonandra*, *Demosthenesia* has the more primitive stamens characteristic, in my opinion, of the group of *Thibaudia*. Therefore, if staminal

characters are to be maintained as indicating phylogenetic history, we cannot combine *Demosthenesia* with *Pellegrinia* unless the genera *Thibaudia*, *Siphonandra*, and their allies are all combined. It is perhaps regrettable that so many small genera appear desirable in Thibaudieae, but as I have already remarked (loc. cit., p. 327), these small genera may well represent the ends of old and not very successful lines of evolution. In my opinion, the taxonomy of the group is clarified by the recognition of these genera.

The second group of the thibaudioid species of "*Pellegrinia*," occurring from northern Colombia to southern Ecuador, will be known as *Plutarchia*. This genus differs from *Demosthenesia* by its articulate calyces which are sharply contracted at the base, being obprimisatic rather than distinctly obconical. In habit it is usually more compact and sclerophyllous than *Demosthenesia*. The phylogenetic import of the presence or absence of an articulation between calyx and pedicel has not yet been sufficiently studied by an anatomist. Its use as a generic character may well be questioned, but I believe the distinct geographic ranges of *Demosthenesia* and *Plutarchia* indicate their distinct phylogeny.

Taxonomic notes on the three genera follow:

PELLEGRINIA Sleumer, Notizbl. 12: 287. 1935.

P. grandiflora has been designated as the type species.

PELLEGRINIA COCCINEA (Hoer.) Sleumer, Notizbl. 12: 288. 1935.

Ceratostema coccineum Hoer. Bot. Jahrb. Engler 42: 317. 1909.

PELLEGRINIA GRANDIFLORA (R. & P.; Don) Sleumer, Notizbl. 12: 288. 1935.

Ceratostema grandiflorum R. & P.; Don, Gen. Syst. 3: 863. 1834.

Ceratostema longiflorum Lindl.; Lem. Fl. Serr. Jard. I. 4: 346b. pl. 353. 1848.

Ceratostema Urbanianum Hoer. Bot. Jahrb. Engler 42: 319. 1909.

PELLEGRINIA HIRSUTA (R. & P.; Don) Sleumer, Notizbl. 12: 288. 1935.

Ceratostema hirsutum R. & P.; Don, Gen. Syst. 3: 863. 1834.

Ceratostema cordifolium Dun.; DC. Prodr. 7: 553. 1839.

Thibaudia hirsuta R. & P.; Dun.; DC. Prodr. 7: 553. 1839, as synonym.

Ceratostema oblongifolium Dun.; DC. Prodr. 7: 553. 1839.

Ceratostema Lobbii A. C. Smith, Contr. U. S. Nat. Herb. 28: 337. pl. 2. 1932.

Pellegrinia Lobbii Sleumer, Notizbl. 12: 288. 1935.

PELLEGRINIA HARMSIANA (Hoer.) Sleumer, Notizbl. 12: 288. 1935.

Ceratostema Harmsianum Hoer. Bot. Jahrb. Engler 42: 317. 1909.

DEMOSTHENESIA gen. nov.

Calyx cum pedicello continuus, tubo obconico, limbo suberecto quam tubo longiore, lobis plerumque 5 deltoideis; corolla subcylindrica, glabra vel pilosa, saepe ampla, lobis plerumque 5 parvis; stamina 10 corollam plus minusve aequantia, plerumque alternatim inaequalia, filamentis distinctis pilosis (pilis laxe patulis), antheris submembranaceis, loculis leviter granulosis, tubulis quam loculis 2-5-plo longioribus amplis flexilibus per rimas elongatas dehiscenibus; stylus filiformis saepe exsertus. Frutices, foliis parvis subcoriaceis breviter petiolatis obscure nerviis, stipulis plerumque aristatis mox deciduis; inflorescentiae axillares, floribus 1-3 pedicellatis.

The genus is named after the Grecian orator Demosthenes. It consists of seven known species, which are found in the high Andes from central Peru to northern Bolivia. *D. Mandoni* is designated as the type species. The genus belongs in the group of *Thibaudia*, from which it is distinct on the basis of its continuous calyces with elongate lobes, its often ample corollas, its usually slightly dimorphic stamens, its elongate tubules, and its stipules.

Demosthenesia buxifolia (Field. & Gardn.) comb. nov.

Ceratostema buxifolium Field. & Gardn. Sert. Pl. 1: pl. 7. 1844.

Thibaudia microphylla Lindl. Gard. Chron. 1848: 23. 1848.

Themistoclesia buxifolia Kl. Linnæa 24: 42. 1851.

Pellegrinia buxifolia Sleumer, Notizbl. 12: 288. 1935.

Demosthenesia Pearcei (Britton) comb. nov.

Rusbya Pearcei Britton, Bull. Torr. Club 20: 68. 1893.

Anthopterus Pearcei Drude; Engl. & Prantl, Pflanzenfam. Nachtr. 4¹: 270. 1897.

Ceratostema Pearcei A. C. Smith, Bull. Torr. Club 60: 111. 1933.

Pellegrinia Pearcei Sleumer, Notizbl. 12: 289. 1935.

Demosthenesia microphylla (Hoer.) comb. nov.

Ceratostema microphyllum Hoer. Bot. Jahrb. Engler 42: 316. 1909.

Pellegrinia microphylla Sleumer, Notizbl. 12: 288. 1935.

Demosthenesia Graebneriana (Hoer.) comb. nov.

Ceratostema Graebnerianum Hoer. Bot. Jahrb. Engler 42: 315. 1909.

Pellegrinia Graebneriana Sleumer, Notizbl. 12: 288. 1935.

Demosthenesia fabulosa (Sleumer) comb. nov.

Ceratostema fabulosum Sleumer, Notizbl. 12: 120. 1934.

Pellegrinia fabulosa Sleumer, Notizbl. 12: 289. 1935.

Demosthenesia Mandoni (Britton) comb. nov.

- Ceratostema Mandoni* Britton, Bull. Torr. Club 20: 137. 1893.
Ceratostema Pilgerianum Hoer. Bot. Jahrb. Engler 42: 318. 1909.
Ceratostema sanguineum Hoer. Bot. Jahrb. Engler 42: 318. 1909.
Pellegrinia Mandoni Sleumer, Notizbl. 12: 288. 1935.

Demosthenesia spectabilis (Rusby) comb. nov.

- Ceratostema spectabile* Rusby, Bull. N. Y. Bot. Gard. 4: 404. 1907.
Pellegrinia spectabilis Sleumer, Notizbl. 12: 288. 1935.

PLUTARCHIA gen. nov.

Calyx cum pedicello articulatus, tubo obprismatico basi saepe abrupte contracto, limbo suberecto tubum aequante vel quam tubo 2-4-plo longiore, lobis 5 deltoideis vel lanceolato-deltoideis; corolla subcylindrica, lobis 5 parvis; stamina 10 corollam subaequantia, filamentis aequalibus vel alternatim leviter inaequalibus plerumque parce pilosis, antheris submembranaceis, loculis leviter granulosis, tubulis quam loculis 2-4-plo longioribus amplis flexilibus per rimas elongatas dehiscentibus; stylus corollam subaequans. Frutices saepe compacti, foliis parvis coriaceis breviter petiolatis obscure nerviis, stipulis aristatis vel saepe ut videtur nullis; inflorescentiae axillares 1-3-flores saepe basi bracteis parvis paucis cinctae, floribus pedicellatis.

The genus is named after the Grecian historian Plutarch. It consists of six known species, and seems to be limited to the high Andes of Colombia and Ecuador. *P. rigida* is designated as the type species. The genus is related to *Thibaudia* and *Demosthenesia*, being distinct from the latter primarily by its articulate calyces. It also shows certain features suggestive of *Cavendishia*, and perhaps indicates a close relationship between that genus and *Thibaudia*.

Plutarchia coronaria (Linden) comb. nov.

- Ceratostema coronarium* Linden; Hook. f. Bot. Mag. Curtis 92: pl. 5575. 1866, as synonym.
Thibaudia coronaria Hook. f. Bot. Mag. Curtis 92: pl. 5575. 1866.
Themistoclesia coronilla Lind. & André, Illustr. Hort. 17: 176. pl. 33. 1870.
Pellegrinia coronaria Sleumer, Notizbl. 12: 288. 1935.

Plutarchia Rimbachii (A. C. Smith) comb. nov.

- Ceratostema Rimbachii* A. C. Smith, Phytologia 1: 130. 1935.
Pellegrinia Rimbachii Sleumer, Notizbl. 12: 289. 1935.

Plutarchia speciosa (André) comb. nov.

Ceratostema speciosum André, Illustr. Hort. 17: 52. pl. 9. 1870.

Pellegrinia speciosa Sleumer, Notizbl. 12: 288. 1935.

Plutarchia rigida (Benth.) comb. nov.

Ceratostema rigidum Benth. Pl. Hartw. 220. 1846.

Ceratostema dichogamum Cuatr. Trab. Mus. Nac. Cienc. Bot. Madrid 26: 10. f. 5. 1933.

Pellegrinia rigida Sleumer, Notizbl. 12: 288. 1935.

Pellegrinia dichogama Sleumer, Notizbl. 12: 289. 1935.

I have carefully compared a photograph and the description of *Ceratostema dichogamum* with Hartweg's type at Kew, and am unable to find any differences.

Plutarchia pubiflora (Wedd.) comb. nov.

Ceratostema pubiflorum Wedd. Chlor. And. 2: 181. 1855.

Pellegrinia pubiflora Sleumer, Notizbl. 12: 289. 1935.

Plutarchia guascensis (Cuatr.) comb. nov.

Cavendishia guascensis Cuatr. Trab. Mus. Nac. Cienc. Bot. Madrid 26: 8. f. 3. 1933.

Ceratostema colombianum A. C. Smith, Phytologia 1: 130. 1935.

Pellegrinia guascensis Sleumer, Notizbl. 12: 289. 1935.

Ceratostema guascense Cuatr.; Sleumer, Notizbl. 12: 289. 1935, as synonym.

Species excluded from *Pellegrinia*, not included in *Demosthenesia* or *Plutarchia*:

Pellegrinia longepedicellata (Sleumer) Sleumer, Notizbl. 12: 289. 1935
(*Ceratostema longepedicellatum* Sleumer, Notizbl. 12: 56. 1934) = SEMIRAMISIA FRAGILIS A. C. Smith.

Pellegrinia parvifolia (Benth.) Sleumer, Notizbl. 12: 289. 1935 (*Ceratostema parvifolium* Benth. Pl. Hartw. 220. 1846) = THIBAUDIA PARVIFOLIA (Benth.) Hoer.

Pellegrinia lanceolata (Benth.) Sleumer =

Periclesia lanceolata (Benth.) comb. nov.

Ceratostema lanceolatum Benth. Pl. Hartw. 142. 1844.

Pellegrinia lanceolata Sleumer, Notizbl. 12: 288. 1935.

In preparing my monograph I had not seen the corollas and stamens of this plant, which was keyed as a very distinct species of *Ceratostema*. A second sheet of the type, in the herbarium of the Royal Botanic Gardens, Kew, bears corollas, which have since been examined by me. The following notes should be considered with the description recently published (loc. cit., p. 344):

Corolla thin carnose, 33–40 mm. long, 5–7 mm. in diameter, densely pale pilose (hairs 0.5–0.8 mm. long) without, glabrous within, the lobes 5, oblong-lanceolate, subacute, 10–12 mm. long, about 4 mm. broad at base; stamens 10, nearly as long as corolla, the filaments glabrous, lightly connate in a tube about 2 mm. long, the anthers rigidly erect, the sacs granular, 8–10 mm. long, incurved at base, the tubules membranous, rigid, very slender, about 0.3 mm. in diameter near apex, about 20 mm. long, opening by oblique pores about 0.5 mm. long; style filiform, about as long as corolla.

The species cannot be left in *Ceratostema* (*Englerodoxa*), nor can it be placed in *Pellegrinia*, from which it is excluded by the articulate calyx and the lack of retrorse hairs on the filaments. Its stiff slender tubules remove it from *Plutarchia*. Its proper place in *Periclesia* is indicated by the glabrous connate filaments, the stiff slender tubules opening by oblique pores, the articulate large-lobed calyx, and the subterminal 2- or 3-flowered inflorescence (the flowers not being solitary as previously described). In addition, the plant bears a marked habital resemblance to the only previously recognized species, *Periclesia flexuosa* A. C. Smith, from which it differs by its pilose branchlets and leaves, its 5-merous flowers, narrower less membranous calyx lobes, shorter filaments, etc. The inclusion of a species with 5-merous flowers does not weaken the genus *Periclesia*, which depends primarily upon a combination of calyx, anther, and habital characters not found in its allies.

Cavendishia Martii (Meissn.) comb. nov.

Thibaudia Martii Meissn.; Mart. Fl. Bras. 7: 173. 1863.

Cavendishia paniculata Rusby, Mem. Torr. Club 4: 215. 1895, and other synonyms listed in my monograph (loc. cit., p. 482).

Having examined a photograph of the type of *Thibaudia Martii*, I find it necessary to replace the well-known *Cavendishia paniculata* by an older name. The two types are essentially similar. The older type, said to have been collected in Brazil, was more likely from southern Peru, in the Amazon drainage basin.

CAVENDISHIA STROBILIFERA (HBK.) Hoer. Bot. Jahrb. Engler 42: 279.
1909.

Thibaudia strobilifera HBK. Nov. Gen. & Sp. 3: 272. 1818, and other synonyms listed in my monograph (loc. cit., p. 509).

Cavendishia acuminata (Hook.) Hemsl. Biol. Centr. Amer. Bot. 2: 272. 1881 (*Thibaudia acuminata* Hook. 1837, and other synonyms listed in my monograph (loc. cit., p. 503, 504)).

Having recently examined the type of *Thibaudia strobilifera* in the herbarium of the Museum d'Histoire Naturelle, Paris, I find it substantially identical with the widespread *Cavendishia acuminata*, which name consequently must be replaced.

POLYCLITA gen. nov.

Calyx coriaceus cum pedicello continuus, tubo obprismatico basi longe attenuato lobis 5-angulato vel anguste alato, limbo erecto tubum subaequante, lobis 5 brevibus; corolla carnosae cylindrica, lobis 5 parvis; stamina 10 aequalia corollam subaequantia, filamentis brevibus basi leviter cohaerentibus, loculis granulosis rigidis gracilibus, tubulis quam loculis paullo brevioribus amplius flexilibus per rimas elongatas dehiscentibus; stylus crassus corollam subaequans. Frutex, foliis coriaceis breviter petiolatis; inflorescentiae axillares subfasciculatae vel brevissime racemosae, floribus 2-6 pedicellatis.

The genus is named after the Grecian sculptor Polyclitus. It is apparently monotypic, known only from the type collection from Bolivia.

Polyclita turbinata (Kuntze) comb. nov.

Chupalon turbinatum Kuntze, Rev. Gen. Pl. 3²: 190. 1898.

Thibaudia turbinata Hoer. Bot. Jahrb. Engler 42: 272, 1909.

Explanation of figures

Fig. 1. Flower of *Pellegrinia hirsuta*.

Fig. 2. Stamen of *Pellegrinia hirsuta*, ventral surface.

Fig. 3. Stamen of *Pellegrinia hirsuta*, dorsal surface.

Fig. 4. Stamen of *Pellegrinia hirsuta*, lateral surface.

Fig. 5. Flower of *Demosthenesia Mandoni*.

Fig. 6. Stamens of *Demosthenesia Mandoni*, ventral surface.

Fig. 7. Stamen of *Demosthenesia Mandoni*, dorsal surface.

Fig. 8. Flower of *Plutarchia rigida*.

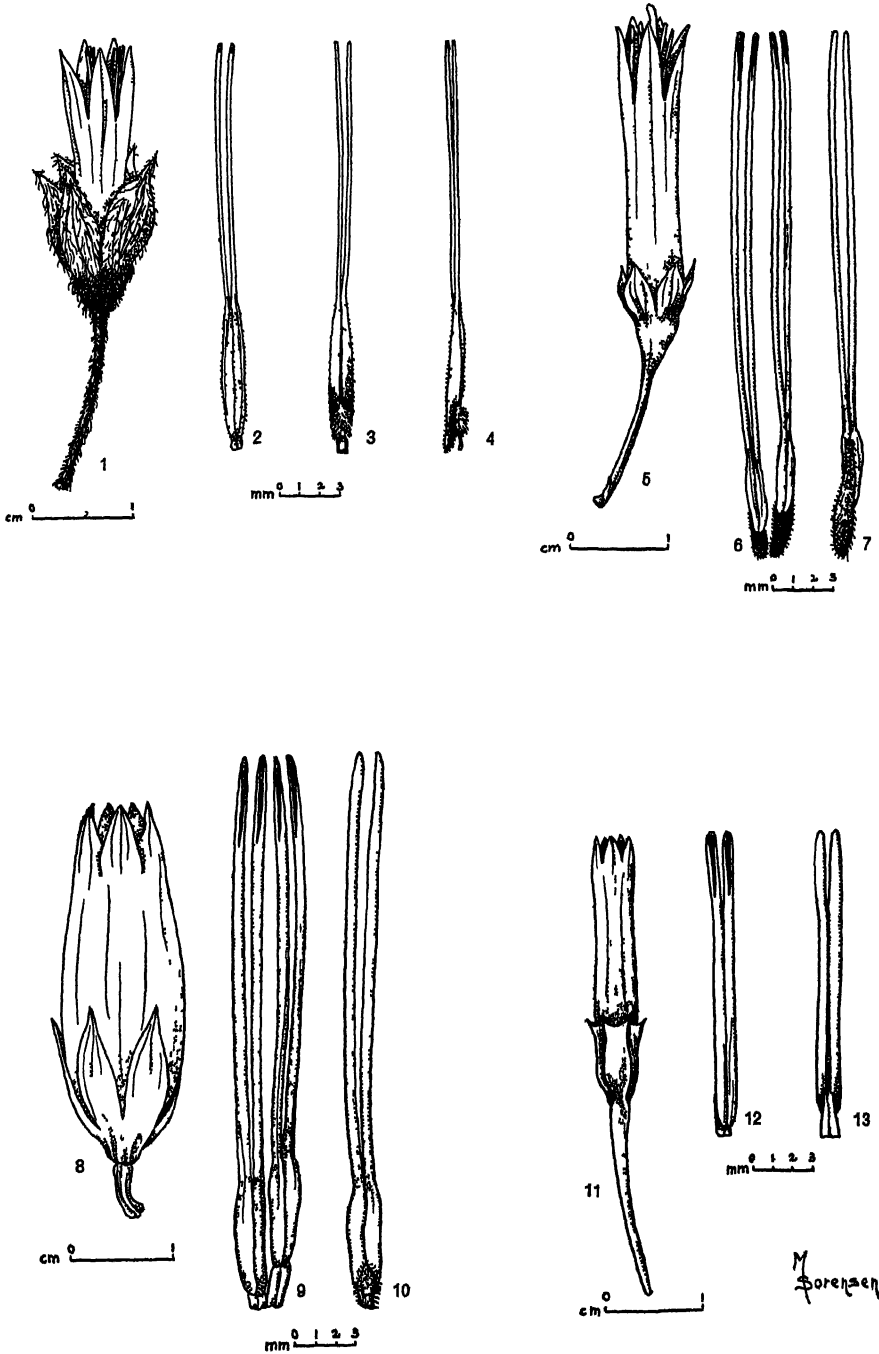
Fig. 9. Stamens of *Plutarchia rigida*, ventral surface.

Fig. 10. Stamen of *Plutarchia rigida*, dorsal surface.

Fig. 11. Flower of *Polyclita turbinata*.

Fig. 12. Stamen of *Polyclita turbinata*, ventral surface.

Fig. 13. Stamen of *Polyclita turbinata*, dorsal surface.



This unique plant is distinguished from *Thibaudia* primarily by the form of its calyx, which is much elongated, continuous with the pedicel, and conspicuously angled, the angles corresponding with the lobes. In the Section *Agathothibaudia* of *Thibaudia*, the calyx is also continuous with the pedicel, but in that section, as in the remainder of *Thibaudia*, the calyx is rounded at base and the inconspicuous angles are opposite the sinuses. The alliance of *Polyclita* with *Thibaudia* is clearly indicated by the form of the anthers, which have short broad cylindric flexible tubules dehiscent by elongate clefts. The genus *Anthopterus* agrees with *Polyclita* in having the calyx winged to the lobes, but the wings are very conspicuous and veined and the corolla is also winged and membranous.

The genus *Thibaudia*, as constituted in my recent paper (loc. cit., pp. 410-439), contains several elements which are held together primarily by anther structure. These elements are: 1. Section *Agathothibaudia* (species no. 1, 2); 2. *Thibaudia turbinata* (species no. 3, here referred to *Polyclita*); 3. Species no. 4-19, among which such species as *T. apophysata* Hoer. and *T. involucrata* A. C. Smith are extremely anomalous, each marked by one or more unique morphological characters; 4. Species no. 20-23, with paniculate inflorescences; 5. Species no. 24-40, a coherent group into which falls the type species of *Thibaudia*. It is conceivable, and perhaps desirable, that some future monographer recognize these many elements as genera, such a course perhaps being conducive to a clearer understanding of American Vacciniaceae. Of these groups, *Thibaudia turbinata* is so distinct that it cannot be left in *Thibaudia*, even permitting the most liberal interpretation of that genus.

NEW YORK BOTANICAL GARDEN

Further fossil studies of the Two Creeks Forest Bed, Manitowoc County, Wisconsin

L. R. WILSON

(WITH ONE TEXT-FIGURE)

In 1930-1931 a detailed study of one hundred feet of the exposed forest bed southeast of Two Creeks, Manitowoc County, Wisconsin, was made (Wilson, 1932). The glacial and ecological histories were discussed and shown to be an important phase in the biotic conditions associated with the later advances of the Wisconsin ice sheets. At that time it was noted that other exposures existed several miles northward in the clay banks on the lake shore. These exposures when investigated proved to have a slightly different history from those of the more southern exposure. The soils upon which the fossil forest developed are in places sandy instead of a heavy red clay. The soils above the forest bed horizon are varied and indicate that they were deposited in ponded glacial waters. With ecological and glacial conditions differing slightly from the southern exposure the present investigation was undertaken in hope that a fuller biological knowledge of the Forest Bed Subinterval might be gained.

Several field trips, during the past three years, have been made to the northern exposures where materials were collected for further study. In June 1933 and May 1934 one portion approximately thirty feet in length was critically examined for organic remains, and the results recorded are from this part of the forest bed. The location of this exposure is on the lake shore approximately seventy-five yards south of the Kewaunee-Manitowoc County line in Section 2, Township 21 North, Range 24 East.

GEOLOGY

Though the soils below the forest bed were not completely exposed, it is assumed that the general features of the geology at the northern exposure of the Two Creeks Forest Bed are the same as at the exposure three miles southward. These may be briefly outlined in their historical sequence as follows: (1) The ice of the Third Wisconsin Substage (Cary) deposited till, which is exposed near the base of the cliffs when not covered by slumped soils from above. (2) The Cary ice front then melted northward beyond the Straits of Mackinac, forming a glacial lake known as the Glenwood Stage of Lake Chicago in the basin of Lake Michigan and varved clays were deposited on top of the till. These varves are quite distinct near the lower contact but disappear toward the top, indicating a change in the lake conditions. As the result of drainage through the Straits of Mackinac the lake level fell to a level probably below the present one of

Lake Michigan (3) The forest, now represented by fossils at Two Creeks, Manitowoc County, Wisconsin, established itself upon the land thus exposed above the lake (4) Ice of the Fourth Wisconsin Substage (Mankato) began to advance from the Patrician center upon the region, water was ponded throughout the forest, and sediments were deposited over the area in the various thicknesses (5) The area was then overridden by the ice and till was deposited over the sediments causing much folding and disturbance (6) Upon the retreat of the Mankato Ice varved lake clays and some sands were irregularly deposited over the till. (7) Subsequent wave work has exposed the forest bed as it appears today.



Fig. 1 Forest bed horizon with spruce log and stump *in situ*

At one place in the northern exposure the soils immediately below the forest bed are stony. This condition has not been seen at any other place, and it might be suggested that these soils originated from till borne on an iceberg in Early Lake Chicago, which grounded at this place

The events which took place during the destruction of the forest at this particular location are complex. Complete explanation cannot be attempted with present data. However, a few tentative conclusions concerning the deposits above the forest bed are worth recording. The deposit immediately overlying the forest bed remains is a layer of red calcareous clay about one-half inch in thickness. This deposit seems to indicate deep water. Overlying the clay is a layer of sand containing much silt. This varies from eight to fourteen inches in thickness (fig. 1). Above the sand

another layer of red clay is found. This is about eight inches in thickness and has a blocky structure. In these deposits organic remains are surprisingly scarce until the top of the second layer of clay is reached. Here are found a few spruce needles and twigs. Above this clay there is a coarse silty sand containing much organic matter. The top of this deposit is indistinct in its contact with what appears to be a very sandy till. Many logs from the forest bed are found near this upper contact usually partly buried in each deposit, but also often completely buried in one or the other. As in the case farther south, the majority of the logs point southwest-northeast.

One log, seven feet long (fig. 1), was found partly attached to its stump, and leaning at an angle of forty-five degrees. No other log has ever been found as nearly upright as this one. It was not completely pushed over because at this particular place in the fossil forest about three feet of sedimentary deposit accumulated before the ice reached the spot. When the ice did override the area it apparently pushed this tree over to an angle of forty-five degrees in the soft mud and sand. Then it tore off the portion which protruded from the sediments leaving a shredded and twisted end to the log. This shredded character of the wood is indicative of live or very recently killed timber.

FOSSILS

The remains of fossil organisms are found in abundance at the more northern exposure and constitute, with the exception of mollusca, nearly the same organisms as are found at the southern exposure of the forest bed.

Spruce wood in form of logs, twigs, and bark is the most abundant type of fossil material. It occurs both in the forest bed horizon and above in the sediments and till. Most of the logs are four to six inches in diameter and the number of annual rings range from sixty to one hundred and forty-two. The oldest log previously found has only eighty-two annual rings. A few logs were found that are about twelve inches in diameter, but these do not have more than eighty to one hundred and twenty annual rings. All logs examined showed a marked decrease in the width of the annual rings near the bark. This apparently is due, at least for those trees that grew at the present exposure, to excessive ponding of water about their trunks as the Mankato Ice advanced southward.

Needles and cones of spruce are present, though the latter are comparatively scarce. The cones belong to the species black spruce, *Picea mariana* (Mill.) BSP., as presumably do the logs and needles. There is a possibility that some of the larger logs are white spruce, *Picea glauca*

(Moench.) Voss., but there is no definite proof at present for this statement.

In the sediments three feet above the forest bed were found fragments of twigs of balsam fir, *Abies balsamea* (L.) Mill., with their needles attached. This species of tree has not previously been recorded in buried Pleistocene deposits of Wisconsin. The only explanation that can be given is that the twigs and needles were transported from a more northern location with the sediments in which they occur. There is evidence at the southern exposure of such transportation in the occurrence of a rock-dwelling moss and a large log that does not show the narrow annual rings at the outside.

Only seven species of mosses were found in the northern exposure as compared with nineteen in the southern. Apparently the local conditions are to be considered as the limiting factor. The moss material was submitted to Mr. L. S. Cheney, of Barron, Wisconsin, who identified the following species: *Bryum bimum* Schreb., *Calliergon turgescens* (Jens) Kindb., *Camptothecium nitens* Schp., *Campylium stellatum* (Schreb.) Bryhn., *Ditrichum flexicaule* Hampe, *Drepanocladus revolvens*, var. *intermedius* (Lindb.), and *Scorpidium Scorpioides* (L.) Limpr. All of these species except the var. *intermedius* of *Drepanocladus revolvens* have previously been recorded from the Two Creeks Forest Bed.

The microscopic plant fossils were observed only in the forest bed level and were studied after the usual manner employed by paleo-ecologists (Erdtman, 1931). The forest bed horizon is about two inches thick, with the upper one-half inch composed of mosses and spruce forest litter and the lower one and one-half inches is mainly silt and organic material of sedimentary origin, and is leached. The whole horizon was separated into four levels as follows: (1) lowest silt containing organic tissues, (2) silt in contact with the forest litter, (3) lower forest litter and, (4) upper litter and mosses in contact with the calcareous clay overlying the forest bed. These samples were dissected for macroscopic tissues and then prepared for microscopic examination.

In the two lowest levels no pollen or spores were found but in the forest litter comparatively large quantities of spruce (*Picea*) pollen occurs. Two very thick-walled guard cells of the type commonly found in the sedges were also found in the litter, but aside from these no other species have been found as microfossils. In the southern exposure one pollen grain of jack pine (*Pinus Banksiana*), two pollen grains of birch (*Betula* sp.), one of a heath and one spore of a fern (*Asplenium* sp.) were found, but none of these species have been found in the present exposure. Because of

the scarcity of jack pine and birch pollen it was suggested that these had been blown into the forest from a distance.

An analysis of the peat suggests that the forest was probably a solid formation of upland spruce. The floor of the forest appears to have had a very sparse covering of moss, sedges and dead spruce needles. The animal fossils are rare except for shell remains of protozoa. These occur in the sediments below the forest litter; genera represented in lowest levels are *Diffugia* and one resembling *Nodosaria*, while in the highest level only *Diffugia* was found. In the lower forest litter several mites were observed, but not identified. One log that has bark beetle excavations upon it was excavated from the sedimentary deposits above the forest bed. These apparently were made by only one genus or species of beetle.

No mollusca were found in the present exposure, while at the southern location eight species were identified and the deposit contained many individuals.

ECOLOGICAL HISTORY OF THE NORTHERN TWO CREEKS EXPOSURE

The ecological history of the northern exposure of the Two Creeks Forest Bed begins with the development of a shallow body of water probably at the time when the Cary Ice front was melting back beyond the Straits of Mackinac and Early Lake Chicago was being drained. In this shallow body of water aquatic animals began to establish themselves. At the location under discussion there occurred only protozoans as far as can be established by the fossil remains. At the more southern exposure however, several species of mollusca were found in the silt below the forest bed, and it is possible that these likewise occurred here, but as yet have not been found. The protozoans represented as fossils are necessarily those that build shells, which persist after the death of the organism. Two genera occur in the silts below the forest litter, and the former is much more abundant than the latter.

As the water level dropped the number of protozoan shells decreased until near the contact of the silt and forest litter none were found. This absence may be due to the brief weathering of the top soils which occurred on dry land, but the interval was too short for a definite soil profile to develop.

When dry land was formed sedges and mosses became established probably at the same time or shortly before the colonization by spruce trees. Black spruce and possibly white spruce became established in a solid formation upon the soils of the area. The forest thrived for more than one hundred years before any deterioration was noted by the decreasing

width of the growth rings in the logs. Some trees may have become infected with bark beetles at this time as one rather large log collected at this location, as well as one at the southern exposure showed bark beetle excavations. Mites also appear to have been abundant during the forest stage.

As the Fourth Wisconsin or Mankato ice sheet began to advance southward, it blocked northward drainage of Early Lake Chicago through the Straits of Mackinac and the water rose in the Lake Michigan basin. Conditions in the forest bed became wetter for wet land and mosses developed abundantly. There is a reappearance of the *Diffugia* shells, indicating the presence of shallow standing water. Then there was a general influx of water over the area and the forest was drowned and buried several feet deep in lacustrine sediments.

THE TWO CREEKS FOREST IN LIGHT OF RECENT PALEO-ECOLOGICAL WORK IN WISCONSIN

In the earlier paper discussing the Two Creeks Forest Bed and its climatic indication it was stated that two conflicting pieces of evidence were present in the form of the prevailing ranges of the plants and the prevailing ranges of the animals. It was suggested that the animal evidence might to some extent be discredited, because those represented in the forest bed as fossils belong to technical groups whose absolute ranges are still imperfectly known. Now, it appears that a reconsideration of the plant evidence might bring about a closer agreement with that of the animals.

Recently, considerable peat pollen work has been done in Wisconsin that furnishes information bearing on the ecology of the Two Creeks Forest Bed. Two deposits of peat have been studied which apparently began to form upon the recession of the Third Wisconsin or Cary Ice, as did the peat at Two Creeks. The best argument for this statement is the presence of peat at the forest bed, for it is logical to assume that peat or organic sediments were forming in ponded areas of the same age if it was possible for peat to accumulate on high ground such as that upon which the forest bed developed. The two deposits referred to above are located, one near Waupaca, Waupaca County, Wisconsin (Voss, 1931); the other, near Lodi, Columbia County, Wisconsin (Truman, 1933). Unlike the peat at the forest bed, these two deposits were not covered upon the advance of the Fourth Wisconsin or Mankato Ice, consequently they should contain not only a record of the flora existing near them at the formation period of the Two Creeks Forest Bed, but also that which existed during the advance of the Mankato Ice and subsequent time. If this is true, then

it is possible to trace the vegetation in its development up to recent time and compare the components of each including those of the fossil forest.

At the bottom of the Waupaca deposit Voss reports finding pollen of *Picea*, *Abies*, *Pinus*, *Quercus*, *Tilia*, and *Ulmus*. The first two genera each make up 40% of the spectrum, *Pinus* 10%, *Quercus*, *Tilia* and *Ulmus* together 5%, and 5% of other species. Truman records 26% *Picea*, 4% *Abies*, 1% *Pinus*, 24% *Larix*, 20% *Gramineae*, 10% *Alnus*, and 15% other species of pollen at the bottom level in the Lodi deposit. The pollen spectrum at the northern exposure of the Two Creeks Forest Bed is 100% *Picea* while at the southern exposure it is 97.5% *Picea*, 1% *Betula*, 0.5% *Pinus*, 0.5% *Asplenium*, and 0.5% *Ericaceae* computed from a count of two hundred fossils. Though it is still early in the stage of investigation, these observations suggest the following picture of the vegetation in eastern Wisconsin during the interval between the Third and Fourth Substages of the Wisconsin glaciation.

On the eastern side of the state near Lake Michigan the forests were dominantly *Picea* while to the westward and southward *Picea* and *Abies* were associated with *Pinus* and several species of deciduous trees. Farther southward *Picea* and *Abies* occurred in still lesser quantity and *Larix*, other deciduous trees and the herbaceous flora were more abundant. If this is true description of the vegetation it might be possible to explain such a distribution on the basis of climatic conditions. However, it may also be explained as an illustration of plant succession governed by physiography and speed of migration similar to the present conditions in Alaska (Rigg, 1934).

Today the northern part of Wisconsin is a floral transitional region, where species of the Canadian Flora meet elements from the Alleghanian, Prairie and Coastal Plain floras. The dominance of the Canadian flora may possibly be explained by the presence of a very young topography throughout most of the region. This is responsible for the ecological conditions which are favorable to the northern type of vegetation, while climate seems to be only a secondary factor of plant distribution in Wisconsin.

There might be some question concerning the larger number of plant species appearing in the basal levels of the two deposits reported on by Voss and Truman than found in the forest bed. If the two areas were colonized by *Picea* and *Abies* before the other trees arrived at the respective locations, why then is there not a level recorded in the bogs equivalent to that shown at the forest bed? In explaining this it is necessary only to point out that both the Waupaca and Lodi basal deposits were formed in ponds and the forest bed peat was formed above water. Though the deposition of sediments might be comparatively uniform in the bodies of

water, the first organic sediments in contact with the mineral soils are deposited rather irregularly. Greater disturbance of microfossils takes place in water than on land and consequently the stratigraphy cannot be as accurate.

Truman, in discussing a possible correlation of one level in the Lodi peat deposit with the Two Creeks Forest Bed states, "The writer suggests that the two high points in the frequency of *Larix* may correspond to successive readvances of the ice [Fourth and Fifth Wisconsin Substages or Early and Later Mankato], and that the intervals of low frequency preceding and separating them characterized by the presence of *Picea* and *Pinus* may be comparable to interglacial periods such as that represented in the development of the Two Creeks Forest Bed described by L. R. Wilson (1932) in which he finds *Picea* the dominant forest component."

The pollen graph presented by Voss for the Waupaca bog does not show any fluctuation of its components that would lead one to make any correlation with the two later ice advances such as is made by Truman. It may be that there was no effect upon the existing vegetation by the readvances of the ice fronts at that location, or that his samples of peat were not collected close enough together to show such fluctuations.

In a study (unpublished) of ten bogs associated with the Glacial Great Lakes in Douglas County, Wisconsin, the writer found that the earliest vegetation in the region was *Picea* and *Pinus*. As the levels of the Glacial Great Lakes became progressively lower with halts of considerable duration at each stage, *Picea* followed on the newly exposed soil as the pioneer tree. It was found that other tree pollens appeared at levels in the bogs a little above the bottom indicating that succession was taking place. Each stage of the Glacial Great Lakes was first bordered by a *Picea* forest a few miles wide while beyond that grew trees belonging to later stages of succession. Such a forest succession cannot be considered as climatically controlled. This development of the forests in the Lake Superior region may be a clue to what would have happened in the fossil forest at Two Creeks had the time interval been somewhat longer.

SUMMARY

1. The exposure here discussed belongs to the same time interval and was connected with the more southern exposure of the Two Creeks Forest Bed described in an earlier paper.

2. The same general geological history is evident at both locations but the northern exposure shows thicker deposits of sedimentary materials over the forest bed before it was overridden by the Mankato Ice.

3. The fossil forest is composed entirely of spruce which developed in some places on sandy soil and at other places on rocky clay.

4. The ecological history suggested by the fossils is, (a) a shallow pond in which occurred protozoa and probably other invertebrates, (b) a spruce forest containing trees of 4 to 12 inches in diameter with as many as 142 annual rings, mosses, sedges, mites, and wood boring beetles, (c) wetter conditions with water mosses and *Diffugia*. This is essentially like the ecological history of the southern exposure.

5. The fossil evidence as a climatic index is discussed in the light of recent investigations, and it is suggested that though the fossil plants have a decided boreal character they also represent the pioneer organisms of denuded areas under certain conditions and are therefore not reliable indicators of a severe climate.

The writer wishes to express his appreciation to Mr. L. S. Cheney for the identification of the mosses and to Mr. F. T. Thwaites and Dr. N. C. Fassett for their helpful criticism and discussions during the course of the work.

COE COLLEGE,
CEDAR RAPIDS, IOWA

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The genus *Delphinium* in North America: series *Pelligerae* of subsection *Subscaposa*

JOSEPH EWAN

Delphinium has apparently undergone long-continued fragmentation in western North America, having differentiated into what may be termed "series," that is, species-groups characterized by a morphological character of the seed or flower. Such series have phylogenetic significance and each is marked by a distribution which is both characteristic and separate. The present paper treats of those species which inhabit the interior deserts of the southwestern United States, constituting what is here defined as the series *Pelligerae*. They share a peculiar seed character, namely, that the dark-bodied seed is wholly enveloped by a white-papery pellicle, often ample and much exceeding the dimensions of the seed proper. The five species here considered are set apart from the cismontane *Delphiniums* of the Pacific Coast by this papery-tegumented character of the seed. Hints as to the mechanics of this process of fragmentation or speciation in the genus have come to mind as the study has proceeded. These suggestions are discussed under each species treated.

The studies here recorded were begun at the University of California at Los Angeles at the suggestion of Dr. Carl Epling to whom I extend my gratitude. In addition to the material there, large and important collections were made available by the United States National Herbarium and by the following California herbaria: Stanford University, the University of California and the working collection of Dr. W. L. Jepson there, Pomona College, the California Academy of Sciences, the Los Angeles (County) Museum (including the Davidson Herbarium), the Santa Barbara Museum of Natural History, and by Mrs. Marjorie Clary of Coachella and Mr. Frank W. Peirson of Altadena. Critical material and types were generously loaned by the New York Botanical Garden. Mr. C. A. Weatherby kindly supplied data and photographs upon repeated requests from the Gray Herbarium; in a like manner Dr. Theodor Just of Notre Dame University, from the Herbarium Greeneanum. Several friends have collected and placed at my disposal pertinent material which has always proved of value or interest. I express my appreciation to all these many contributing botanists, curators and friends for this unstinted co-operation.

HISTORICAL NOTE

Of the five species treated here two are of widespread distribution; three are highly restricted endemics. It is partly by reason of this that

much of the confusion has arisen. The earliest published species of the series *Pelligerae* is *D. scaposum* of Greene (1881), a plant hardly to be confused with others of its region, although long made to include the rarer subscape forms of *D. amabile*. It is a widespread and distinct element of the Arizona flora and not to date positively known from California.

Prior to this, however, the second widespread species of the Great Basin (*D. amabile*) had been known as *D. azureum* of Michaux (1803). This was a misconception, however, for Michaux's species does not occur west of the Rocky Mountains but ranges from the south Atlantic states to the central Mississippi Valley and northward to Saskatchewan. It is upon the varied interpretation of this widespread Great Basin species that the confusion in the published treatments has arisen.

In 1887 Gray published his "attempt to distinguish the North American species." In this six-page paper Gray provided no descriptions of the five newly proposed species, but relied solely upon the diagnoses provided by a synoptical key. Consequently subsequent botanists have found it difficult, indeed, to interpret Gray's inadequately characterized proposals. Among the species proposed was *D. Parishii* based upon a collection made at Palm Springs, Riverside County, California. This endemic is restricted to a small area along the western margin of the Colorado Desert of California. Nevertheless, as interpreted by most subsequent authors, Gray's name was made to embrace forms as far east as southern Utah. In 1912 Rydberg published *D. coelestinum* based on Edward Palmer's collection at St. George, Utah. He, along with some subsequent authors, later attributed to it forms of the southern Great Basin and its westward extension, the Mohave Desert. Such a view is correct. However, as pointed out by Tidestrom (1925), the name is not valid but a homonym in the genus. Accordingly he proposed the name *D. amabile* by which this widespread species is properly known. Another element of confusion was added by reason of the fact that the type of *D. coelestinum* and hence of *D. amabile* was collected at its easternmost limit, for the plants of that region are not typical of the species as it occurs more abundantly to the west.

Hence there were described from nearly opposite corners of the western deserts two *Delphinium* species, each in turn being interpreted by various authors up to the present as embracing the populations lying between these points. It is true that two species are here involved. As mentioned above, however, *D. Parishii* is much restricted and does not occur through the wide range ordinarily attributed to it.

With such unpropitious beginnings and the well known variability among its species, leading Brewer and Watson (1876) to remark that "the species of this genus are variable in so many directions that it is difficult to satisfactorily limit or define them," our western *Delphiniums* have re-

mained poorly understood despite the summation of the North American species by Gray (1895) and by Davis (1900), of the southern California species by Davidson (1908) or that of the species for the entire state by Jepson (1915).

The five species treated here lie within the diverse aggregate designated by Huth in 1895 as "Tribus Subscaposa" (hereinafter designated as "Subsection Subscaposa," an alteration to conform to Art. 12, Intern. Rules of Bot. Nomencl., 1930), which embraced such unlike species as *D. decorum*, *Parishii*, *nudicaule* and *camporum*. In spite of its comprehensive nature Huth's treatment of the genus is, in general, coherent and determinate even with respect to the North American species which he knew but sketchily from limited herbarium materials.

USE OF THE CATEGORY SUBSPECIES

The category subspecies has been adopted here since the author believes that: (a) it expresses relationship, in the same way that "subgenus" relates itself to genus, and has the advantage over the term "variety" of being at once oriented with respect to established taxonomic grouping, (b) it connotes emergence, or the recent origin in geologic time of the phase from a larger parent plexus, and that (c) it escapes confusion attending the use of the category "variety" in both scientific and popular usage, from the inexact horticultural sense to its use in systematic botany where it may vagrantly represent at one time a mere color variant or other minor morphological form, or again may serve as equivalent of the present concept "subspecies." The author is cognizant that the term "variety" is currently employed by many workers in exactly the sense here attributed to the category "subspecies." It is felt, however, that the use of the latter term, in growing favor among investigators who have adopted it essentially for the reasons outlined above, has sufficient advantages to be deserving of wide use.

TERMINOLOGY

The leaf blade of the *Delphinium* species here treated is normally cut into three or five principal divisions. These I have termed the primary segments. They in turn are variously incised or lobed usually once, sometimes twice, rarely more, and such lobes are referred to as the ultimate segments. The ultimate segments may sometimes be even pectinate. Nipple-mucronate refers to a white nipple-like mucro or callosity occurring at the apex of the whole blade alone or at the apices of the ultimate segments. Flower length equals the extreme measurement from spur-tip to tip of the sepal most nearly on the same plane with it. And likewise, sepal length equals the extreme measurement from the thickened summit

of the pedicel to the tip of a lateral sepal (commonly somewhat larger in both dimensions than the upper or lower sepals). Follicle length does not include the cusp, which is of variable length in different species and within the same species.

Subsection Subscaposa nom. nov.

Tribus *Subscaposa* Huth, Engler's Jahrb. 20: 445. 1895.

Series Pelligeræ series nov.

Semina perspicue integumentis laevibus amplissimis niveis atque chartaceis nequaquam alatis neque squamosis neque transverse rugoso-squamellatis.

Desert-dwelling perennials of scapose or subscapose habit with seeds distinctly inclosed within a smooth loose crepe-white papery pellicle—never winged, echinate nor “becoming transversely rugose-squamellate.”

KEY TO THE SPECIES OF SERIES PELLIGERÆ

- A. Sinuses of the lower petals 3–4 mm. deep; leaves strictly basal, with a close pubescence or glabrous, the primary segments obovate or even subspatulate, the ultimate segments broadly rounded, nipple-mucronate; flowers clear dark or royal blue; Arizona and contiguous Nevada and New Mexico. 1. *D. scaposum*
- AA. Sinuses of the lower petals less than 2.5 mm. deep; leaves predominantly cauline (if basal then plants decidedly hairy or pale-flowered), the primary segments linear to broadly cuneate-oblongate, the ultimate segments acute or acuminate, apiculate or sometimes nipple-mucronate; flowers blue-purple to whitish; Mono County, Calif. to s. Utah, south to S. Arizona and Lower California.
- B. Stem stout and strict, often hollow, 20–40 cm. tall, arising in well developed plants from a thickened crown with 3–5 woody-fibrous roots; leaves reduced and withering at flowering time and not noticeable or if persistent then thick and somewhat fleshy; drainages of the Mohave Desert and southern part of Great Basin. 2. *D. amabile*
- BB. Stem erect (but scarcely stout) or lax or even reclining, slender, 30–60 cm. tall, arising from a usually single or sometimes two or three fibrous roots, the stem being scarcely thickened into a crown; leaves evident, not withering at flowering time yet not thickish or if withering then linear-pectinate divided; drainages of the Colorado Desert.
- C. Leaves variously hirsute; mature follicle cluster nearly as broad as long (6–12 mm.), subglobose in outline. 3. *D. subglobosum*
- CC. Leaves glabrous and glaucous (occasionally pubescent when young); mature follicle cluster distinctly longer than broad (12–20 mm.), oblong in outline.
- D. Primary leaf divisions narrowly oblong (aver. 4–7 mm. wide medially) with the ultimate segments linear-divided; flower dark blue or purple. 4. *D. collinum*
- DD. Primary leaf divisions broadly cuneate (aver. 8–15 mm. wide medially) with ultimate segments broadly lobed; flowers azure blue. 5. *D. Parishii*

1. **DELPHINIUM SCAPOSUM** Greene

Delphinium scaposum Greene, Bot. Gaz. 6: 156. 1881, based on specimen collected by Greene at Gila Bluffs, New Mexico, 25 IV 1881 (date changed by Greene from 1880 over the printed label). Type, as indicated by Greene (Calif. Acad. Sci. Herb. no. 233), examined.

D. decorum F. & M. var. *scaposum* Huth, Helios 10: 33. 1893.

Strikingly scapose perennial, herbage light grass-green, glabrous or nearly so (esp. in early season specimens) or with a close even chamois-like pubescence, never hirsute or coarsely pubescent; stems erect, usually one- to few-stemmed or occasionally freely branching from the base, 30–45 cm. tall, arising from a slender woody-fibrous rootstock; leaves wholly basal (rarely also cauline in plants from northern parts of its range), decorative, pentagonal or triangular in outline, with 3 to 5 primary divisions, these cuneate-obovate or subspatulate with few ultimate teeth or lobes, these nipple-mucronate; raceme open, 5–10-flowered; flowers 22–28 mm. long, the sepals intense royal blue (spur commonly darkening in age in the herbarium to a darker bronzy color, the remainder blue, thus characteristically bicolored), or a lighter bright blue, lanceolate, abruptly acute, 13–15 mm. long, the upper petals white, blue-tinged or -tipped, emarginate, the lower petals dark blue, their blades ovate, cleft below the middle to form a nearly closed but deep sinus 3–4 mm. deep; follicle cluster ovate or oblong, 10–20 mm. long, glabrous; seeds dark brown with a sordid white-membranous papery pellicle.

Representative material: NEW MEXICO: Grant Co.: Hills along the Gila, *Greene* 25 IV 1880 (or 1881). McKinley Co.: (Old Fort) Wingate, *Matthews* (fide Huth). ARIZONA: Pima Co.: Tucson, *Toumey* in 1894; Baboquivari Mts., *Fosberg* 7463; Covered Wells (5 mi. w.), *Fosberg* 7462. Gila Co.: San Carlos, *Ethel Palmer* in 1932 (albino but with usual dark spur!). Yavapai Co.: Skull Valley, *Jones* in 1903; Prescott, *Peebles & Harrison* 4001. Coconino Co.: Flagstaff, *Purpus* 7073. Mohave Co.: Yucca, *Jones* 3894; Peach Sprs., *N. C. Wilson* in 1893. UTAH: Kane Co.: Kanab, *Jones* 5286a. Washington Co.: Springdale, *Jones* 5237. Grand Co.: Moab, *Eastwood* in 1892. Sevier Co.: Vermillion, *Jones* in 1901. COLORADO: Montezuma Co.: Mancos, *Eastwood* in 1892. Montrose Co.: Paradox, *Walker* 74. Delta Co.: Delta (mesa west), *Tidestrom* 2193. NEVADA: Clark Co.: Eldorado Canyon at Nelson, *Jones* in 1907.

This handsome species with racemes of rich royal blue flowers is certainly the most striking of the deserticolous *Delphiniums*. Two recognizable races of this species, outlined below, appear over its range. They conform so closely with the topography of Arizona resulting from great geomorphogenic adjustments which produced its two major river systems that perhaps those races may have developed simultaneously with this change in the earth's crust.

Race a. Flowers deep royal blue, raceme fairly compact; plants always scapose; follicle cluster ovate in outline, 10–13 mm. long; drainages of the Gila River and Mogollon Mesa.

Race b. Flowers often lighter blue, raceme diffuse; plants not strongly scapose, often branching; follicle cluster oblong in outline, 18–20 mm. long; drainages of the Colorado River and Colorado Plateau.

From the western counties of Arizona and along its northern border come collections which variously combine these characters, however, and consequently for the present I only suggest these races. Still, almost any collection can be placed in one of these two categories, or conversely, it is possible upon the characteristic combination of tendencies to place a given collection geographically. The New Mexican and southern Arizona collections cited above are of the first race while the remaining constitute the paler-flowered "race b." The Newberry collection, which I have not seen, mentioned by Greene in the original description, is doubtless "race b." This is said to have come from "south of Diamond River," which is probably the place of that name in the Grand Canyon country described by Lemmon (Overland Monthly 12: 253 of ser. 2. 1888).

Regarding the poisonous properties of this species, Miss Eastwood remarks that she has seen in the vicinity of Mancos, southwestern Colorado, four or five cattle lying together in a field, bloated as the goat-skin water jugs of Palestine.

2. *DELPHINIUM AMABILE* Tidestrom, Contr. U. S. Nat. Herb. 25: 207. 1925.

Stout upright perennial, simple or branching from base, frequently hollow, 20-40 (or 90) cm. tall, arising from a short thickened rootcrown upon a few strong deep-seated rhizomatous roots clothed by persistent fibrous leaf bases; herbage often reduced and inconspicuous, pale green, variously hirsute-pubescent to glabrous and glaucous but never with a close-knit pubescence; leaves prevailing on only lower half of stem (or evenly cauline or wholly basal), long petioled, deltoid in outline, angulately divided to the base into usually 3 or 5 cuneate divisions, these again cleft into linear early infolded lobes; racemes oblong, compact but not crowded, 8-16 (or 30) flowered, flowers 20-25 (seldom only 16) mm. long, on stout pedicels, the sepals lance-oblong, rather obtuse, often puckered or crimped at the tip, averaging 8-12 mm. long, not concolorous but variously light blue (clear sky-blue only in ssp. *apachensis* and dark blue-purple in some montane races), the upper petals merely notched, whitish, the lower petals bluish, the claw sometimes thinly pubescent with short glandular hairs, the blades with sinuses 1.5-2.5 mm. deep, a little less than half their length, usually open, often villous with curling white hairs; follicles nearly straight, commonly with divergent cusps, finely puberulent but shining, 8-14 (or 21) mm. long; seeds almost black, 2-4 mm. long, the coat a cocoon-like clear-white papery pellicle, deeply impressed at distal end and ample at the angles.

Authors have treated the common *Delphinium* of the Great Basin as *D. amabile*, but that it represents the same species as the plant of the Mohave Desert has not been suggested, except by inference in synonymy. S. B. Parish has outlined (1930, 487) the relation of the Mohave Desert

to the Great Basin point by point. He says, "there are no natural obstacles to cut [the Mohave Desert] from the deserts of southern Nevada and Utah, parts of the Great Basin, whose climatic conditions are like its own, and of which it may be justly considered a part." The true cause for the chorologic (in Rùbel sense) diversity of the Mohave and Colorado deserts was also suggested by Parish to rest in the topography of the deserts themselves. Thus the Mohavan area is a complex of several basins, resulting from Pleistocene lakes for the most part, while the Colorado Desert is derivative from the single fairly uniform Cahuilla Basin and its catchment area. Apparently there have been developed within many of these Mohavan basins local races of *Delphinium amabile*, distinguishable by color shades, flower size, degree of stoutness and relative persistence of leaves at anthesis. The Manix Lake region northeast of Barstow shows a form of this species having unusually robust habit and loose racemes. On the other hand there occurs, as a geminate species, the essentially undifferentiated *Delphinium Parishii* on the Colorado Desert at lower elevations for the most part, the average elevation of the Mohave Desert being two-thousand feet whereas the Colorado Desert rests at an approximate sea-level elevation.

In *Delphinium amabile* there is possibly reached the ultimate in xerophytic habit among the North American species. When the aridity of this interior basin (including, accordingly, the Mohave Desert) is fully realized the reduction in vegetative parts to be noted in this species is less surprising. There are historically recorded drought periods of thirty-two months duration without registerable precipitation, with intervals between effective rains of even greater magnitude. Jaeger refers (1933, 133) to one such drought of 1909-1912 and its withering but not fatal effect on the Creosote Bush in the Bagdad region of the Mohave Desert. It is certainly the ability of such xerophilous types as *Delphinium amabile* to withstand protracted wilting and recover from it unimpaired upon the recurrence of the brief winter rains that have enabled these desert species to persist since the beginnings of Pleistocene time.

From rarer *Delphinium Parishii* of the Colorado Desert, *D. amabile* may be distinguished by its much stouter habit, pubescent generally reduced or inconspicuous leaves and darker blue flowers in dense racemes. Again, *D. amabile* favors typically rocky knolls and open desert mesas, ascending canyons of bordering mountains only on margins of its range, whereas *Delphinium Parishii* occurs only in canyons of mountains bordering the Colorado Desert on west or about washes issuing from them. This peculiarity in the distribution of *D. Parishii* is, I believe, associated with the fact that the Cahuilla Basin has been filled by water so recently that the spread of the species to the desert floor is imperceptibly slow.

KEY TO THE SUBSPECIES OF *D. AMABILE*

- A. Sinuses of the lower petals 2–2.5 mm. deep, the lobes distally spreading; stems glabrous and glaucous (commonly bluish); racemes elongated, loose, 20–45 cm. long; south-central Arizona. 2a. *D. amabile apachensis*
- AA. Sinuses of the lower petals 1.5–2 mm. deep, their lobes not conspicuously spreading; stems variously pubescent, less often glabrous; racemes moderately dense, little elongated; widespread in the southern Great Basin.
- B. Flowers usually bright blue; sepals 8–14 mm. long; leaves withering at flowering time, mostly pubescent, their segments seldom mucronate, the margins early involute 2b. *D. amabile typicum*
- BB. Flowers pale (whitish or tinged with blue); sepals 6–7 mm. long; leaves evident at flowering time, mostly glabrous, their segments nipple-mucronate, plane to margins. 2c. *D. amabile pallidum*

2a. *Delphinium amabile* subsp. *apachensis* (Eastw.) comb. nov.

Delphinium apachensis Eastw., Proc. Calif. Acad. Sci. ser. 4. 20: 142. 1931, based on *Eastwood* 17144 from road betw. Apache Lodge and Packard, Gila Co., Ariz. Type (Calif. Acad. Sci. Herb.) examined.

Smooth-stemmed perennial, often bluish below, more or less glaucous, firm but less stout than ssp. *typicum*; herbage glabrous or subglabrous, often somewhat fleshy; leaves both cauline and basal; raceme rather loose, full-flowered, 20–45 cm. long; flowers clear azure blue, the sinus of the lower petals 2–2.5 mm. deep, their lobes crimped, tending to spread giving a lacerate aspect to flower; follicles maximum size for species; seeds with pellicle ashy or discolored.

Collections examined: ARIZONA: Pinal Co.: San Tan Mts., *Harrison* 3533; Superstition Mt., *Peebles, Harrison & Kearney* 3895. Gila Co.: Roosevelt Dam, *Eastwood* 8665. Maricopa Co.: Apache Trail, *Eastwood* 6271; Salt River Mts., *Gillespie* 5578.

The full-flowered racemes of azure blue flowers suggest certain strains of cultivated *Delphiniums* for their beauty. The sepals, contrary to original description, are 9–12×5 mm. (in type collection) and ovate. This is a segregate of fairly sharp distinction which may be distinguished from the typical plant of the deserts to north and west by the remarkably deep petal sinuses. The plant tends to hold its leaves longer through the flowering period than ssp. *typicum*.

2b. *Delphinium amabile* subsp. *typicum* nom. nov.

Delphinium amabile Tidestrom, Contr. U. S. Nat. Herb. 25: 207. 1925, based on following homonym:

D. coelestinum Rydb., Bull. Torr. Club 39: 320. 1912, based on *Edward Palmer* "11" from "southern Utah," 1877. Type (Columbia Univ. Herb. at N.Y. Bot. Gard.) examined. From a ms. list of his collections of year 1877, made out by Dr. Sereno Watson and available at Gray Herba-

rium, it will be noted that no. 11 is "*Aconitum nasutum*" whereas no. 10 is "*Delphinium azureum*" from "St. G." This is St. George, Utah, and may be therefore known as the type locality. An isotype (U. S. Nat. Herb. 2009) examined where the label is more legible shows this correction to be borne out. The paratype, an Arizona specimen, *Palmer* 3, 1876, also represents this species. (Not *D. coelestinum* Franchet, 1894.)

D. azureum Michx. var. *vimineum* [(Don) Gray misapplied by] Coville, Contr. U. S. Nat. Herb. 4: 57. 1893. as to Argus Mts. (*Coville & Funston* 737) which is by examination exactly this ssp.

D. Parishii [Gray misapplied in part by] Davis, Minn. Stud. Bot. 24: 441. 1900; Jepson. Fl. Calif. 1: 526. 1915; Davids. & Moxley, Fl. S. Calif. 142. 1923; Wilde, Cornell Univ. Agric. Exp. Sta. Bull. 519: 64. 1931.

D. scaposum [Greene misapplied by] Brandegee, Zoe 5: 148. 1903 as to plants of Providence Mts., Calif.

D. mohavense Parish ex Jepson, pro synonym., Fl. Calif. 1: 526. 1915.

Erect, typically stout rigid perennial 20–50 cm. tall, stems greenish or bluish above and pallid or white below, more often pubescent, sometimes strongly hirsute; leaves rather inconspicuous, reduced upwards and all early withering or involute; raceme more or less compact (in plants from vicinity of Barstow often loose), flowers light blue (in plants from Mono and Inyo counties and montane S. Calif. dark blue), sepals oval, plane, not recurved at tip, commonly with median band of pubescence, spur 8–12 mm. long, curving or straight, acute or acutish; pellicle of seeds clear white.

Representative material: UTAH: Washington Co.: betw. St. George and Beaverdam Mts., *Tidestrom* 9306; La Verken, *Jones* 5196a. Utah Co.: Goshen *Jones* in 1880. NEVADA: White Pine Co.: Muncy, *Jones* in 1906. Mineral Co.: Mt. Grant, *Heller* in 1913. Nye Co.: Rhyolite, *Shockley* 68. Clark Co.: St. Thomas (12 mi. s.), *Tidestrom* 9084; Moapa, *Kennedy* 1104; Good Sprs., *K. Brandegee* in 1915; Logan, *Kennedy* in 1909; Kyle Canyon, Charleston Mts., *Jaeger* in 1926. ARIZONA: Mohave Co.: Hualpai Mts., *Braem* in 1927; Franconia, *Jones* in 1903. Coconino Co.: Grand Canyon, *Lemmon* in 1884. Maricopa Co.: Wickenburg, *Jones* in 1903. Pima Co.: Vail (15 mi. se.), *Fosberg* 7942. CALIFORNIA: Mono Co.: Black Canyon, White Mts., *Duran* 527; Sherwin Grade, *Feudge* 142. Inyo Co.: Red Hill west of Bishop, *Heller* 8247; Shepherds Canyon, Argus Mts., *Coville & Funston* 737; Pleasant Canyon, Panamint Mts., *Hall & Chandler* 6968; Lee Well, Nelson Range, *Hall & Chandler* 7136; Black Mts., Death Valley, *Jaeger* in 1927. Kern Co.: Willow Sprs., *Munz* 10036; Cameron, *Feudge* 142. Ventura Co.: Frazier Borax Mine, *Abrams & McGregor* 209. Los Angeles Co.: Kings Canyon, Liebre Mts., *Dudley &*

Lamb 4350; Mt. Pacifico, San Gabriel Mts., *Peirson* 8441; Lytle Creek Canyon, *Hall* 1462. San Bernardino Co.: Kramer, Mohave Desert, *Parish* 9710; Victorville, *Spencer* 346; Fremonts Pk., *Hall & Chandler* 6860; Providence Mts., *Cooper* in 1861 (small flowered), *T. Brandegee* in 1902, *Munz, Johnston & Harwood* 4128 and *Hoffmann* in 1930 (all typical). Riverside Co.: Cottonwood Sprs., *Pierson* 7897.

Typical *Delphinium amabile* (here designated merely for easy reference as ssp. *typicum*) ranges from the open deserts and rocky hillsides of the desert ranges to the bordering mountains and ascends their slopes, through the piñon belt, to at least 7400 feet at the fringes of the Transition and Canadian zones. The most characteristic feature is the whole rigid aspect of the plant—stem, petioles and pedicels. The expanded (green) blades of the leaves in sterile plants are pubescent with white hairs only along veins and midrib or ciliate. But on withering the leaves (now colorless or brownish) show white spreading hairs up to 1 mm. in length, flat and as seen with binocular suggestive of shredded coconut, as covering the whole blade which has now become involute. Sometimes hirsute- and nearly glabrous-leaved plants occur in the same colony however; any correlation between this distinctive growth form in the genus and this type of pubescence is therefore impossible to draw.

There are two montane races of this subspecies which differ in such noticeable respects from the typical plant of the Sonoran deserts below that I am characterizing them here. They occupy two isolated areas in Southern California.

Race a. Habit taller (to 90 cm. high!), virgate; flowers usually dark, colored, smaller, more numerous, in often elongated subspicate racemes. North side of San Bernardino Mts. in Bear Valley region: Big Bear Lake, *Davidson* 2199, *Parish* 3781, *Jones* in 1900 and *J. T. Howell* 2748 from "open forest" on north shore. Also at Baldwin Lake, *Hilend* 469 and *Peirson* 10675, in Holcomb Valley, *Munz* 10659 (referred to *D. Parishii* var. *pallidum* by *Munz*, Bull. S. Calif. Acad. Sci. 31: 61) and at Cactus Flat in Cushenbury Canyon, 6000 ft., *Jones* 12 V 1926. This race was confused with *D. recurvatum* Greene by *Davidson* (Muhl. 4: 34). I am of the opinion that this race is clearly related to *D. amabile* however. There is pressing need for field study here. Though I have collected in the Bear Valley region during four summers I have not encountered this *Delphinium*. Presumably it occurs as either isolated plants or in small colonies.

Race b. Habit from strictly scapose to scarcely at all scapose; herbage moderately pubescent to strongly hirsute; inflorescence loosely racemose (racemes 20–40 cm. long), at times branching below to form secondary racemes (15–20 cm. long); flower color inconstant, various shades of light blue to pink purplish, petals often contrastingly snow-white. Component of variable populations about Mt. Pinos, Ventura County, as Cuddy Valley, *Dudley &*

Lamb 4515 and *Epling & Dunn* 27 VI 1931 and "road to saw-mill," *Dudley & Lamb* 4605. It is to be noted that ssp. *pallidum* occurs in this same area. This is the perplexing form referred to by Jepson (Fl. Calif. 1: 525) under *Delphinium hesperium* var. *cuyamacae* (Abrams) Jepson with the words "perhaps also on Mt. Pinos." Its singular dark-flowered forms bear striking resemblance to *Delphinium Parryi* Gray of cismontane Southern California. The lax racemes are at once a noticeable feature of this race. As with "race a" a fortified explanation of this race is at present impossible by virtue of several minor points of interdisagreement among the available collections.

2c. *Delphinium amabile* subsp. *pallidum* (Munz) comb. nov.

D. Parishii Gray var. *pallidum* Munz, Bull. S. Calif. Acad. Sci. 31: 61. 1932, based on *Munz* 6954 from Seymour Creek, Mt. Pinos, 10 VI 1923. Type (Pomona College Herb. 20509) examined.

? *D. Hansenii* (Greene) Greene var. *kernense* Davidson, Muhl. 4:37. 1908, based on *Hasse & Davidson* 1703 from "dry sunny slope," Mt. Cummings, Tehachapi Mts., 10 VI 1907. Type (Los Angeles Mus. Herb. 3976) examined. This represents a form with shaggy white-pilose leaves and lower petals scarcely emarginate but flower size and color are exactly this ssp. Lacking the critical seeds this Tehachapan element must await further field study and collections; it seems unlikely, however, that it is related to *D. Hansenii*.

Stout simple-stemmed perennial, commonly 20–35 cm. high; leaves mostly basal, generally glabrous, subsucculent, the segments nipple-mucronate; raceme fairly dense, flowers whitish or tinged with blue, the sepals short and obtuse, somewhat recurved at tips, thus giving a blunt aspect to flower, 6–7 mm. long, evenly pubescent over back with short white hairs, spur short, 7–10 mm. long, blunt at tip.

Other collections examined: Cuddy Valley, Mt. Pinos, *Epling & Dunn* 8 VI 1931, *Dudley & Lamb* 4527; Seymour Creek, *Peirson* 3589 ("mostly in open"); Goodenough Mdw., *Dudley & Lamb* 4722.

This subspecies occupies the Mt. Pinos region of California—an area of perennial interest to the biologist for its endemism and mixed distributional affinities. This *Delphinium* is characterized, as pointed out by Munz, by its pale flowers and short sepals and spur.

3. *DELPHINIUM SUBGLOBOSUM* Wiggins.

Delphinium subglobosum Wiggins, Contr. Dudley Herb. 1: 99. pl. 7. 1929, based on *Wiggins* 2003 from "open grassy slope near Banner, about 5 miles below Julian," San Diego Co., 20 III 1926. Type (Dudley Herb. 163266) examined.

D. Parryi Gray var. *subglobosum* Munz, Bull. S. Calif. Acad. 31: 61. 1932, in part, excluding "San Felipe" and "Campbells" citations.

Strict, erect, simple or few-branched perennial from slender woody root-stock of few deep-seated fibrous roots; stem glabrous and glaucous or puberulent below, washed blue or purplish, 45–60 cm. high; leaves rather numerous, chiefly basal, long-petioled, blades roundish, the few principal divisions again divided into several strictly linear obtuse or apiculate segments, the petioles (esp. distally) and blades hirsute or hirsutulose with spreading white curling hairs; raceme short (10–18 cm. long), at length rather interrupted but not loose, about 10-flowered, the flowers variable in color, usually dark blue or purplish, stout-pedicelled, the sepals oval, obtuse, 8–11 mm. long, hirsutulose when young, the pubescence persisting as a median band; follicle short, subglobose, truncate at summit, 6–10 mm. long, straw-colored (not greenish at maturity), the cusp short; seeds 1.5–2 mm. long, the pellicle more or less ample, clear white.

Other collections examined: SAN DIEGO COUNTY: Montezuma Valley, Jaeger 26 V 1926 (singular habit and strongly hirsute); Jacumba, near International Boundary, Ferris & Bacigalupi 8222.

Grassy benches and rock pockets of canyons draining into the Colorado Desert, along its western margin, San Diego Co., California. Apparently occurs only at somewhat higher elevations than *Delphinium collinum* which occupies the same region and differs from that species in having pubescent to hirsute leaves, shorter more compact raceme and subglobose blunter follicles.

The position of *Delphinium subglobosum* phylogenetically cannot at present be ventured. From both *collinum* of the desert canyons at lower elevations and from *Parryi* of the cismontane foothills which in this region are broken up to admit the coastal flora to encroach upon the desert associations, *Delphinium subglobosum* seems distinct. The seed character definitely separates it from *D. Parryi* of the coast which belongs to another series of the Subsection Subscaposa. *D. subglobosum* carries the pellicled-type seed of the present series Pelligerac. The collections available are discontinuous geographically and frequently lack mature seeds so do not admit of any assured understanding of the species. Wiggins, who knows the plant best from field experience in the region, states its range, "along the eastern slope of the Laguna and Cuyamaca mountains of San Diego County in the Upper Sonoran Zone, in the *Sabina* [*Juniperus*] *californica* belt" (Flora San Diego County 1: 280–281. 1929. Unpublished thesis, Stanford University).

4. *Delphinium collinum* Ewan sp. nov.

D. Parryi Gray var. *subglobosum* Munz, Bull. S. Calif. Acad. Sci. 31: 61. 1932, in part, as to "San Felipe" and "Campbells" citations.

Slender, erect perennial, 30–70 cm. high, from a slender woody-fibrous rootstock; stem simple or as often branching, commonly bluish, glabrous and glaucous; leaves predominantly basal, of 3 principal sublinear divisions these again divided into few to several shorter, linear, subfiliform, mucronulate teeth, the cauline reduced or inconspicuous, puberulent when young, glabrous in age or nearly so, petioles dilated at base, the lower 8–10 cm. long; racemes elongate, open or early interrupted, the lowermost branches distant; flowers on ascending or spreading pedicels 8–20 mm. long, their sepals dark blue or purplish but bright, oval, rounded or barely acute, 9–12 mm. long, essentially glabrous, the uppermost and spur with fine puberulence or with finely pubescent median band, the upper petals light blue or pallid, the lower petals emarginate (sinus 1 mm. deep), blue-purple, moderately white-villous; follicles oblong, venulose, 12–14 (rarely 10 or 15) mm. long, with prominent cusp, often darker; seeds 2–2.5 mm. long, the white crepe pellicle commonly impressed on the faces to form irregular wing-like angles.

Herba perennis caulibus strictis gracilibus, 30–70 cm. altis, e radice tenui lignosa, simplicibus vel saepe ramosis, caesiis, glabris glaucisque; foliis imprimis ad caulis basim confertis, tripartitis, segmentis sublinearibus divisis dentatis brevioribus linearis ac subfiliformis, mucronulatis; caulibus inconspicuis, omnibus primum puberulentis deinde glabris, inferiorum petiolis 8–10 vel 12 cm. longis; racemis elongatis atque patentibus, ramis inferioribus remotis divaricatis; floribus pedicellis divaricatis vel arcuatis, 8–20 mm. longis, elatis, sepalis atro-caeruleis tamen lucidis, ovalibus, obtusis vel subacutis, 9–12 mm. longis, extus glabris vel ad medium villosulis, petalis superioribus azureis vel fere albidis, inferioribus emarginatis, subniger, albo-villosis; folliculis oblongibus, 12–14 (rarissime 10 vel 15) mm. longis, cuspidate prominentiore ornatis, venulosis, seminibus 2–2.5 mm. longis, integumentis niveis saepe impressis irregulariter angulatis similiter alatis.

TYPE: Ridge betw. Campbells Ranch and Mason Valley, San Diego County, Calif., *Epling & Robison* 4 IV 1932. (Univ. Calif. at Los Angeles Herb.) Isotypes to be distributed.

Rocky slopes of canyon spurs and ridges, associated with *Encelia farinosa*, *Krameria canescens*, *Fouquieria* and *Fagonia* of desert-scrub, along western margin of the Colorado Desert of San Diego County.

Other collections examined: San Felipe Creek, *Pierson* 7740; jct. of Grapevine and San Felipe creeks, *Jepson* 8789; San Felipe Hill, *Jones* 19 IV 1906; Yaqui Well, *Eastwood* 2647; Hellhole Cañon, *Epling & Robison* 5 IV 1932; head of Sentenac Canyon near San Felipe, *Epling & Robison* 5 IV 1932; Campbell Ranch, *Munz & Hitchcock* 12082; Mason Valley, *Duran* 3204; Oriflamme Canyon, *Epling et al.* 22 VI 1932.

The place occupied by *Delphinium collinum* in the present series can best be summarized by the chart given below, showing its morphological relationship to its three nearest geographic allies. *Delphinium Parryi* is a

member of another series characterized by distinctly winged seeds. Although the characters here given are stated decisively a rather wide latitude for variation must be granted in this genus. The notes on flower color have been drawn up wholly from herbarium material on the basis of Ridgway's Nomenclature of Colors, 1886, since, under ordinary care in drying, *Delphinium* specimens keep their natural colors and such notes will therefore have workable uniformity among general collections.

SPECIES	STEMS	LEAVES	SEPAL COLOR	MATURE FOLLICLES
collinum	glabrous	glabrous to puberulent	hyacinth blue or smalt blue	oblong, microscopically puberulent
subglobosum	glabrous	hirsute or hirsutulose	hyacinth blue	subglobose, lightly hairy
parishii	glabrous	glabrous	campanula blue	oblong, wholly glabrous or subglabrous
parryi	thinly puberulent to ashy-hirsutulose	thinly pubescent to hirsutulose	cyanine blue to plum purple	oblong, evenly hairy with fine appressed puberulence (rarely glabrous)

As suggested early in this paper *Delphinium collinum* may have arisen by hybridization between *Parishii* and *subglobosum* following the establishment of *Parishii* at approximately its present position in the western arm of the Colorado Desert. By reference to the above chart its morphological position will be seen to be exactly intermediate between these species, for it combines the glabrous leaves and follicle shape of *Parishii* with flower color and leaf contour of *subglobosum*.

5. DELPHINIUM PARISHII Gray

Delphinium Parishii Gray, Bot. Gaz. 12: 53. 1887, pro parte, based on S. B. & W. F. Parish 1222 from Agua Caliente (now Palm Springs, Riverside Co.) but more exactly from Tahquitz Canyon (or West Canyon) above Palm Springs (cf. Muhl. 3: 125), Colorado Desert, IV 1882. Type (Gray Herb.) photograph and isotypes examined. Excluding reference to "adjacent Lower California" based on C. R. Orcutt from "Mts. of N. Lower Calif." 5 VII 1884; this collection annotated in customary manner by Gray as "*D. Parishii*." From photograph and immature seed specimens kindly provided by Mr. C. A. Weatherby, I can speak only negatively at present, that is, that the Orcutt collection mentioned by Gray (i.e. paratype) is not *D. Parishii*. Its exact relationships are uncertain. I have seen another collection from 40 miles west of Mexicali, 4000 ft., Baja Calif., Munz 9595, with which the Orcutt collection favorably agrees. It possibly represents a southern extension of *D. subglobosum* Wiggins.

D. Parishii [Gray misapplied in part by] Davis, Minn. Bot. Stud. 24:

441. 1900; Jepson, Fl. Calif. 1: 526. 1915, excluding all cited colls. except *Parish* 6074; Wilde, Cornell Univ. Agric. Exp. Sta. Bull. 519: 64. 1931.

Erect or somewhat lax slender perennial, simple or divergently branched, 12–36 cm. high, from slender, fibrous cord-like rootstock; herbage glabrous, often glaucous; lower leaves ample, glabrous or with a few scattered hairs, blades broadly cordate or roundish, 3–8 cm. broad, palmately divided into 3 primary cuneate divisions, each irregularly cleft into 2 or 3 broad oblong rounded (seldom acuminate) but mucronate lobes, petioles sparingly ciliate, 2–10 (or 15) cm. long; upper leaves trifid to midrib into narrowly lanceolate to linear-acuminate divisions, glabrous, long-petioled (.5 to 5 or 10 cm. long); raceme open, loose, few-flowered, 8–30 cm. long, or rarely a loose panicle up to 60 cm. with spreading branches bearing 2–6 flowers at their summits; flowers light or azure blue, pedicels spreading (12–24 mm. long), sepals ovate, glabrate, 8–11 (or 13) mm. long, little surpassing the petals, two-thirds the length of the spur; follicles oblong or ovate, 11–13 mm. long, the cusp prominent; seed 1–2 mm. long, the loose white-crepe pellicle copious.

Collections examined: RIVERSIDE COUNTY: Snow Creek, *W. D. Baker* in 1930; Murray Canyon, *Pearson* 2902; mouth of Tahquitz Canyon, *Johansen & Ewan* 7094; vicinity of Palm Springs, *Parish* 6074 and many collectors; Palm Canyon, *Johnston* in 1917; Deep Canyon, *Clary* 821.

Localized about the western arm of Colorado Desert, California, it favors the banks of streams and gravel benches of canyons draining into the Cahuilla Basin, ascending at least to 2500 feet elevation.

When reviewing the Southern California species, Davidson expressed difficulty in finding agreement between the specimens then before him and Gray's original description (cf. Muhl. 4: 36), unaware that he was dealing in this instance with a highly restricted species erroneously amplified by authors to include the dissimilar Mohave Desert plant. However, he left the matter with the view that only the Palm Springs' collections could justly be taken as *Delphinium Parishii*—which, I believe, is the correct decision.

Gray characterized *D. Parishii* as "rigid-stemmed," a situation which disturbed me as unjustified for the species, especially when compared with the truly stout *Delphinium amabile* of the Mohave Desert. His character was taken from the Parish type sheet which shows the leaf-blades almost wholly lacking, decapitated as it were, with only the long petioles stiffly remaining. As the species is thus represented it may be rightly considered "rigid-stemmed"—a leafless gaunt plant and therefore distinctly atypical for this *Delphinium* which is leafy in anthesis with the blades not withered but expanded, green and conspicuous. Upon finally suspecting the possible traumatic nature of this condition I consulted Dr.

R. B. Cowles of the University of California at Los Angeles, a zoologist who has given particular attention to reptiles. He at once suggested that the condition might be due to the browsing activities of the native vegetarian chuckwalla. And this is likely the fate of the leaf-blades of the type specimen! Camp relates finding a chuckwalla in a *Larrea* bush "from which most of the leaves had been stripped" and the remains of *Franseria* and *Euphorbia* in the stomachs of others (Univ. Calif. Publ. Zool. 12: 524. 1916). It may be concluded then that the type collection (for the isotypes examined show the same condition) of *Delphinium Parishii* is not typical of that species.

The "All Saints Bay" (i.e. Todos Santos Bay) record for this *Delphinium* (Syn. Fl. 1: 48. 1895) is rather *Delphinium Parryi* Gray, precisely the maritime form "var. *maritimum* Davidson" (Muhl. 4: 35). This collection was made, not by Orcutt, the logical inference from the citation, but by (Miss) Fanny E. Fish in May 1882, at that time a resident of Sauzal, Baja California. This collection, a photograph and seeds of which have been available to me, is designated by Gray as *Parishii* in the manner in which he indicated type-basis materials and doubtless contributed to his concept of this species.

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The optical properties of some natural gums and resins

A. E. ALEXANDER

Through the courtesy of Dr. Charles L. Mantell and the Gum Importers Association of America, samples of the commoner natural resins used in industry were forwarded the writer for optical study. Appreciation is also extended to Mr. R. A. Young of the Bureau of Plant Industry for kindly straightening out the confusion existing between the trade or locality name and the generic and specific designation of these same commercial terms.

Gums are amorphous and under polarized light such substances react isotropically. They consequently possess only one index of refraction.

Special immersion oils of known refractive index were used and the Becke test employed to obtain the desired optical data. The index of refraction of several of these natural resins, as determined, is:

CW Kauri.....	1.546
#3 Pale Kauri.....	1.546
#3 Brown Kauri.....	1.544
Pale East India.....	1.543
Zanzibar.....	1.542
Rosin.....	1.542
Ivory Congo.....	1.541
Dark Congo.....	1.541
Black East India.....	1.541
Benguela.....	1.541
Pontianak.....	1.540
Loba B Manila.....	1.539
Hard Manila.....	1.539
Bold Dammar.....	1.538
Batu (Batoe).....	1.538
Tacamahac.....	1.538
Ghatti.....	1.528
Senegal.....	1.526
Gutta Percha.....	1.528
Tragacanth.....	1.510 (mean index)

The botanist and the manufacturer using natural gums or resins might be interested in the following data correlating trade or locality names with scientific names and the place or places where these particular trees or shrubs occur. No one textbook so far as the writer knows gives this information in condensed form.

<i>Trade or locality name</i>	<i>Botanical nomenclature</i>	<i>Where found</i>
Accra copal.....	Paradaniella Oliveri.....	Nigeria
Accroides.....	From various species of Xanthorrhoea.....	Australia, Tasmania
Almadina.....	Euphorbia rhipsaloides.....	Tropical Africa

<i>Trade or locality name</i>	<i>Botanical nomenclature</i>	<i>Where found</i>
Amber	<i>Pinites succinifer</i>	Baltic Coast
Animi	<i>Hymenaea courbaril</i>	West Indies, Brazil
Arabic	<i>Acacia senegal</i>	Sudan
Balata	<i>Mimusops balata</i>	Venezuela, Guianas
Black Boy	<i>Xanthorrhoea hastilis</i>	Australia
Brazilian	From various species of <i>Hymenaea</i>	Brazil
Chicle	<i>Achras sapota</i>	
	<i>Vitellaria mammosa</i>	W I, Mex, Cent Am.
Congo Red	<i>Landolphia florida</i>	Tropical Africa
Coumar.	<i>Coumarouna odorata</i>	Tropical America
Damar (Dammar)	<i>Vateria indica</i> , from the genera <i>Hopea</i> , <i>Shorea</i> , <i>Balanocarpus</i> , <i>Vateria</i>	Malay, Sumatra, E I, Netherlands
Elastica	<i>Castilla elastica</i>	
	<i>Manihot glaziovii</i>	
	<i>Ficus elastica</i>	Cent and S Am, Asia
Elemi	<i>Canarium luzonicum</i>	
	<i>Protium icariba</i>	
	<i>Elaphrium elemiferum</i>	Africa, Brazil, Mexico
Frankincense	From various species of <i>Boswellia</i>	Northern Africa
Gamboge	<i>Garcinia morella</i>	Siam
Grass tree	<i>Xanthorrhoea hastilis</i>	Australia, Tasmania
Guaiac	<i>Guaiacum officinale</i> , <i>G. sanctum</i>	Tropical America
Gutta percha	<i>Palaquium gutta</i>	Malaya
Indian	<i>Vateria indica</i>	India
Karaya	<i>Sterculia urens</i>	East Indies
Kauri	<i>Agathis australis</i>	Australia
Macassar	<i>Cananga odorata</i>	Southern India, Java, Philippines, Malay
Manila	<i>Agathis dammara</i>	Australia
Mastic	<i>Pistacia lentiscus</i>	Chios
Myrrh	<i>Balsamea myrrha</i>	India, Arabia, Somali
Sandalac	From various species of <i>Callitris</i>	Australia, N. W. Afr.
Sierre Leone	<i>Copaifera guibourtiana</i>	West Africa
Sumatra (Dragon's blood)	<i>Daemonorops Draco</i>	
	<i>Dracaena cinnabari</i> , <i>D. Draco</i>	Sumatra, Borneo
Tacamahac	<i>Calophyllum tacamahaca</i>	
	<i>Icica heptaphyllum</i>	
	<i>Elaphyrum tomentosum</i>	
	<i>Calophyllum inophyllum</i>	W. I., E. I.
Tragacanth.	<i>Astragalus</i> spp.	Turkey, Persia
Zanzibar	<i>Trachylobium verrucosum</i>	East Africa

Notes on the genera *Basistemon* Turcz., *Hassleropsis* Chod., and *Saccanthus* Herzog

HAROLD N. MOLDENKE

In 1916 Theodor Herzog proposed the genus *Saccanthus*¹ as a new genus of the *Verbenaceae*. On his original collection labels he indicated that his first impression was that the plants might belong in the *Solanaceae*, but when he published the genus he placed it definitely and without question in the *Verbenaceae*, even going so far as to assert that it was closely related to *Rhaphithamnus* Miers. The generic name, *Saccanthus*, he derived from the very saccate corollas, which, he admitted, rendered the genus most unique in the *Verbenaceae* and certainly very distinct from *Rhaphithamnus*. Herzog's material was all from Bolivia.

In the course of my monographic studies of the New World and cultivated *Verbenaceae* I borrowed all available herbarium material of *Saccanthus*, including the original types and three isotypes of each of Herzog's two species, *S. silvaticus* and *S. violaceus*. Study of this material has revealed the very interesting fact that the genus is not verbenaceous, but that it is a member of the *Scrophulariaceae*, series *Antirrhinoideae*, tribe *Hemimerideae*, according to the classification of R. von Wettstein in Engler and Prantl's "Die Natürlichen Pflanzenfamilien," related to the genus *Angelonia* H. & B.

Further researches in the library and in the herbarium have brought to light the genus *Hassleropsis*, proposed in the *Scrophulariaceae* by R. H. Chodat in 1904² on the basis of a Hassler collection from Paraguay. Chodat proposed only one species in *Hassleropsis*, *H. spinosa*, of which, fortunately, type material was available to me in the herbarium at Kew. *Saccanthus violaceus* Herzog and *Hassleropsis spinosa* Chod. are conspecific.

In 1863 Turczaninow published the genus *Basistemon*³ as a new genus in the *Verbenaceae*. In 1876 Bentham and Hooker f.⁴ transferred *Basistemon* Turcz. from the *Verbenaceae* to the *Scrophulariaceae*, giving as the reason for the transfer the position of the ovules and the type of inflorescence. Wettstein, who monographed the *Scrophulariaceae* for Engler and Prantl's "Die Natürlichen Pflanzenfamilien," placed *Basistemon* in the series *Antirrhinoideae*, tribe *Cheloneae*, and stated⁵ that it was closely related to or even synonymous with *Brandisia* Hook. & Thoms. The

¹ Meded. Rijks Herb. Leid. 29: 47.

² Bull. Herb. Boiss. ser. 2, 4: 285.

³ Bull. Soc. Imp. Nat. Mosc. 36: 214.

⁴ Gen. Pl. 2: 1244 (incorrectly cited by Baehni and Macbride as "1826")

⁵ Engl. & Prantl, Nat. Pflanzenfam. 4^{3b}: 66. 1897.

genus has remained in this more or less doubtful status in the *Scrophulariaceae* for 37 years, until, in 1934, Charles Baehni and J. Francis Macbride published a note⁶ establishing the fact that *Saccanthus* Herzog and *Basistemon* Turcz. are congeneric. Baehni and Macbride, however, missed the fact that *Hassleropsis* Chod. is also a generic synonym, and they are entirely in error in their proposal to shift *Basistemon* back into the *Verbenaceae*. Even though both *Basistemon* and *Saccanthus* were originally proposed in the *Verbenaceae*, my own studies of the type collections of all the known species of this genus (including those of *Saccanthus* and *Hassleropsis*) have convinced me that Bentham and Hooker f. were quite right in transferring the genus to the *Scrophulariaceae*. The inflorescence of certain verbenaceous genera is similarly reduced, it is true, and "pendant ovules are not in contradiction to the diagnosis of the *Verbenaceae*" according to Baehni and Macbride. Notwithstanding this, the genus *Basistemon* is definitely scrophulariaceous. No known genus of *Verbenaceae* possesses the conspicuously saccate corollas which it exhibits, although a slight inflation of the lower part of the corolla-tube is noticeable in *Cornutia* and in some other verbenaceous genera. Aside from that, however, the very distinctly axile placentation, numerous ovules, and capsular fruit found in *Basistemon*, definitely exclude it from the *Verbenaceae*, and, along with the plainly 2-celled ovaries, indicate its true position in the *Scrophulariaceae*, in which family woody genera are not at all common. It belongs definitely in the series *Antirrhinoideae* and the tribe *Hemimerideae*, not in the tribe *Cheloneae* as Wettstein supposed. In *Cheloneae* the flowers are neither spurred nor saccate, while in the *Antirrhineae* and *Hemimerideae* they are either spurred or saccate at the base. In the *Antirrhineae*, however, the corolla has a definite tube, which is lacking in the *Hemimerideae*. The plainly saccate tubeless corollas of *Basistemon* therefore clearly indicate its position in the family.

The following notes concerning the five known species of *Basistemon* are worth recording:

(1) *BASISTEMON BOGOTENSIS* Turcz., Bull. Soc. Imp. Nat. Mosc. 36²: 214. 1863. This is the type species of the genus. The type was collected by Jean Jules Linden (no. 812) near Pandi, Cundinamarca, Colombia, in 1842, at an altitude of 2400 feet. An isotype is deposited in the herbarium at Kew and a fragment of an isotype in the Britton Herbarium at the New York Botanical Garden. The specific name was spelled "*bogotense*" by Turczaninow, but under Article 72 of the International Rules (1930) all generic names terminating in the suffix "*-stemon*" must be considered

⁶ Candollea 5: 345.

masculine; hence the spelling of Hooker f. and Jackson [Ind. Kew. 1: 277. 1895] is here adopted.

(2) **BASISTEMON PERUVIANUS** Benth. & Hook. f. Gen. Pl. 2: 1245 (1876) apud Hook. f. & Jacks. Ind. Kew. 1: 277. 1895. *Russelia peruviana* Spruce ex Benth. & Hook. f. Gen. Pl. 2: 1244, in syn. 1876. The type of this species was collected by Richard Spruce (no. 4515) near Tarapoto, San Martín, Peru, in October, 1856. The type and two isotypes are deposited in the herbarium at Kew and a fragment of the type in the Britton Herbarium at the New York Botanical Garden. The binomial, *Basistemon peruvianus*, was not validly published in the 1876 reference to which it is usually cited. In fact, it does not occur there at all, being merely suggested in the text. Spruce's cheironym, however, is given there and also a brief description of the plant. The binomial was apparently first validly published in the "Index Kewensis" in 1895 (although the specific name is there misspelled "*peruviana*"), the citation there given referring to the brief description of 1876 and therefore validating the binomial.

(3) **BASISTEMON SILVATICUS** (Herzog) Baehni & Macbr., Candollea 5: 345. 1934. *Saccanthus silvaticus* Herzog, Meded. Rijks Herb. Leid. 29: 47. 1916. The type of this species was collected by Theodor Herzog (no. 1132) at Villa Montes on the Río Pilcomayo, Chuquisaca, Bolivia, in November, 1910, and is deposited in the Rijks Herbarium at Leiden. Isotypes may be found in the herbaria at Berlin, Stockholm, and Vienna, and a fragment in the Britton Herbarium at New York. The species was also collected by Pearce (s.n.) along the Machuiapo, El Beni, Bolivia, in December, 1864, deposited in the herbarium at Kew. The specific name is misspelled "*silvaticum*" by Baehni and Macbride.

(4) **Basistemon spinosus** (Chod.) Moldenke, comb. nov.

Hassleropsis spinosa Chod., Bull. Herb. Boiss. ser. 2, 4: 285. 1904. *Saccanthus violaceus* Herzog, Meded. Rijks Herb. Leid. 29: 47. 1916. *Basistemon violaceum* (Herzog) Baehni & Macbr., Candollea 5: 345. 1934. The type of this species, which is also the type of the genus *Hassleropsis* Chod., was collected by Emil Hassler (no. 7350) near Concepcion, Paraguay, in September, 1901, and is deposited at Geneva, with an isotype at Kew. The type of *Saccanthus violaceus* was collected by Theodor Herzog (no. 1214) at Charagua, Santa Cruz, Bolivia, in December, 1910, and is deposited at Leiden, with isotypes at Berlin, Stockholm, and Vienna, and a fragment at New York.

In *B. spinosus* the ovules are very numerous in each cell of the ovary, although the fruits examined seem to indicate that most of these ovules never mature, so that the fruits are mostly 1- or 2-seeded. The seeds are densely spiny throughout. In *B. silvaticus*, on the other hand, there seem

to be only 2 or 3 ovules in each cell of the ovary, but, again, axile in their attachment. The stigma in both species is very small and punctiform, mostly very indistinct. The ovary is ellipsoid when young, subglobose in age, glabrous, and slightly lobed. The capsules are 2-valved, but bear on their back several prominent ridges giving the appearance of a 4- or 5-celled capsule before it has opened. The style is persistent on the maturing fruit. In *B. spinosus* the 4 stamens are plainly didynamous, all inserted at the same level near the base of the gamopetalous portion of the corolla, but two plainly much longer than the other two. In *B. silvaticus* the stamens are almost equal in length. According to Herzog the color of the corolla in *B. silvaticus* is white, while in the other species it is violet.

Other differences that might be mentioned between *B. spinosus* and *B. silvaticus* are that in the former species the corolla-sac is densely glandular-pubescent throughout on the inner surface, the flowers are about 4 mm. in diameter, the calyx-lobes are acute (not at all subulate), and the leaves are usually only 1.5–2.5 cm. long and 4–9 mm. wide. In the latter species the corolla-sac is glandular only at its very base within, the flowers are about 6 mm. in diameter, the calyx-lobes are long-subulate, and the leaves are to 4 cm. long and 16 mm. wide. The foliage in the former species mostly blackens in drying and is borne on extremely abbreviated spur-like twigs, while in the latter species it does not blacken and the twigs are elongate.

The anther-connective in *Basistemon* is conspicuously thickened and dilated and assumes a sagittate form. As the pollen-grains mature, the connective spreads farther and farther apart, until, when the anther-sacs dehisce, they lie in practically a straight line at right angles to the filament. The line of dehiscence is a slit on the top of both thecae. The leaves are opposite in all the species. In a letter to the writer from Dr. F. W. Pennell this distinguished authority on the *Scrophulariaceae* expresses his agreement with the findings set forth in the present article and remarks that since the known species of this genus have come to light in such distant portions of South America, viz., Colombia, Peru, Bolivia, and Paraguay, it is very possible that we are just beginning to become acquainted with a considerable South American genus.

(5) *Basistemon Rusbyi* Moldenke, sp. nov.

Fruticulus; ramis ramulisque gracilibus acute tetragonis dense puberulis; nodis non spinosis; foliis sessilibus vel subsessilibus, laminis ovatis vel ovato-ellipticis membranaceis nitidis 1.3–5.5 cm. longis, 1–3.2 cm. latis, acutis vel brevissime acuminatis, margine minute serrulatis, ad basin rotundatis, supra glabris, subtus dense minuteque puberulis; inflorescentiis axillaribus, cymis 1–3-floris bracteolatis; pedicellis 4–6 mm. longis dense puberulis; calyce cam-

panulato 2-2.6 mm. longo glabrato, lobis 5 lanceolatis ad basin amplissimis, 0.7-2.3 mm. longis, ad basin 1.5-1.8 mm. latis, apiculatis costatis; corolla saccata, tubo obsoleto, folliculo ca. 5.2 mm. lato intus extraque glabro, limbo ca. 5.2 mm. lato, lobis intus parce glanduloso-pubescentibus extra glabris; staminibus 4, ca. 0.6 mm. supra basin corollae insertis, didynamis; filamentis complanatis glabris, 2 ca. 1.5 mm. longis, 2 ca. 2.6 mm. longis; thecis antherarum in linea recta divergentibus; stylo paullo exserto ca. 4.6 mm. longo; stigmatibus sub-2-lobatis; ovario elliptico ca. 1 mm. longo et 0.6 mm. in diametro, 2-loculari, in quoque loculo 2 ovulis pendulis ad apicem medii dissepimenti insertis.

The type of this species was collected by Henry Hurd Rusby (*no.* 1343)—in whose honor it is named—at Reyes, El Beni, Bolivia, on October 26, 1921, at an altitude of 100 feet, and is deposited in the herbarium of the Royal Botanic Gardens at Kew, with an isotype and a fragment of the type in the Britton Herbarium at the New York Botanical Garden.

The following artificial key may be found useful in separating the five species discussed above:

1. Corolla-sac densely velutinous within.
 2. Corolla violet, its sac densely glandular-pubescent throughout within; flowers about 4 mm. in diameter; calyx-lobes acute; leaves usually only 1.5-2.5 cm. long and 4-9 mm. wide, mostly blackening in drying, borne on extremely abbreviated spur-like twigs.....*B. spinosus*.
 - 2a. Corolla white, its sac glandular only at the base within; flowers about 6 mm. in diameter; calyx-lobes long-subulate; leaves to 4 cm. long and 16 mm. wide, not blackening in drying, borne on normal elongated twigs.....*B. silvaticus*.
- 1a. Corolla-sac glabrous both outside and within.
 3. Branches spiny; Colombia.....*B. bogotensis*.
 - 3a. Branches not spiny; Peru and Bolivia.
 4. Leaves 1.3-5.5 cm. long, 1-3.2 cm. wide; Bolivia.....*B. Rusbyi*.
 - 4a. Leaves 5.7-14 cm. long, 2.3-8.1 cm. wide; Peru.....*B. peruvianus*.

THE HERBARIUM,

ROYAL BOTANIC GARDENS, KEW

Ephedra Coryi

E. L. REED

(WITH TWO FIGURES)

While on a collecting trip in the early part of July, 1934, the writer discovered an *Ephedra* closely resembling, in habit, *Equisetum arvense* in that it had, above ground, only green profusely-branched stems. A further study of it through the fruiting stages in the spring and early summer of 1935 warrants a description of it as an hitherto undescribed species.

Ephedra Coryi¹ sp. nov. Planta: frutex humilis erectis 1-5 dm. altus; ramis viridibus numerosus erectus 1-4 mm. in diametro; scalis ramulorum 2 ad quemque nodum; vagina facta 1-2 mm. longis; apicibus obtusis 1-2 mm. longis vel subulatis 4-10 mm. longis; amentis mascularis sessibilis vel in ramis brevibus 2-10 mm. longis; bracteis 5 gemini 2 mm. longis; lobis peranthi ad summum coniunctis; columna staminum 3 mm. minusive longis; antheris 6-8 sessibilis aut in filamentis brevis; amentis ovulatis terminalibus in ramis brevibus $\frac{1}{2}$ -4 $\frac{1}{2}$ cm. longis; bracteis 4 gemini 5 mm. minusive longis; bacca rotunda sufflava carnosca esculenta 1.1 cm. minusive in diametro; seminibus 2 ovatis triangularibus exertis.

A slender stemmed, profusely-branched shrub 1-5 dm. high; branches erect, opposite; all above ground stems green, 4 mm. in diameter or less which arise from an upright underground stem whose origin is from a node of an extensive system of rhizomes; aerial stems all short-lived; scales 2 at each node (sometimes 3) connate at their bases forming a sheath 1-2 mm. long, their tips obtuse 1-2 mm. long or subulate 4-10 mm. long; staminate aments in pairs from the axils of the scales or on short branches of the season 2-10 mm. long, sometimes there are 3 staminate aments at the ends of these short stems, 1 terminal and 2 in the axils of its scales; bracts 5 pairs 2 mm. long; slightly united at their bases; perianth lobes united to their summits; anthers usually 8 sessile or the outer ones short stipitate; stamen column 3 mm. long; ovulate aments on the ends of short branches of the season, of 1 or 2 internodes, 0.5-4.5 cm. long; bracts 4 pairs, 5 mm. long or less, becoming fleshy at maturity; fruit a round fleshy, edible, cream-colored berry up to 1.1 cm. in diameter; seeds in pairs, oblong, triangular in cross section, 7 mm. long or less.

In sandy soil among native grasses, in "shinnery" among scrub oak, and occasionally on the gentle slopes of playa lakes. From Meadow to Tahoka south to Big Spring and Andrews, Texas. Specimens have been collected at Meadow, Brownfield, Wellman, Tahoka, O'Donnell, Lamesa

¹ Named in honor of my friend, Mr. V. L. Cory, Sonora, Texas, Range Botanist of the Texas Agricultural Experiment Station.

and near Ackerley, Texas. Type locality: Brownfield, Texas. Type specimens are in the National Herbarium, Smithsonian Institution, Washington, D.C. and in the Herbarium of the New York Botanical Garden, New York City, N.Y.

Its propagation is largely, if not entirely, by an elaborate system of underground rhizomes. A careful study of the seeds of two seasons has so far failed to show any with viable embryos and germination tests have proved equally unsuccessful. It is a "sand binder" and readily adjusts itself to the shifting sands of its habitat.

TEXAS TECHNOLOGICAL COLLEGE
LUBBOCK, TEXAS

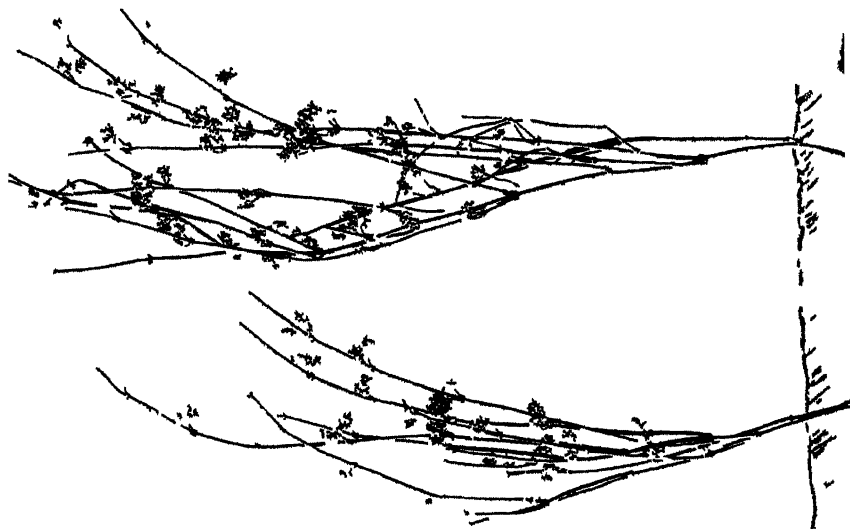


Fig 1 Staminate plant of *Ephedra Coryi*, showing the aments sessile or on short stems of the season $\times \frac{1}{2}$



Fig 2 Ovulate plant of *Ephedra Coryi*, showing the aments on short stems of the season, also a group of mature fruits. $\times \frac{1}{2}$.

INDEX TO AMERICAN BOTANICAL LITERATURE

1931-1936

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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The growth of plant embryos in culture¹

CARL D. LARUE

(WITH FIVE FIGURES)

The growth of immature plant embryos in culture is not new, for Hannig as early as 1904 was able to grow embryos of *Raphanus* and *Cochlearia* to maturity after they had been removed from their ovules when they were about 1.2 mm. long.

Stingl (1907) was able to grow embryos of several grains after removal from their own endosperm, but instead of placing them in culture solutions he transferred them to the endosperms of other species of grains. He found *Secale* endosperms better for the growth of *Triticum* embryos than endosperms of other seeds of *Triticum*. *Hordeum* embryos grew better in *Triticum* endosperms than in their own. This work showed that embryos were not necessarily limited to the nutrition supplied by endosperms of their own species.

Knudson (1922) showed that the seeds of orchids could be germinated without the presence of symbiotic microorganisms if sugar were supplied.

Dietrich (1924) followed Hannig's lead in the cultivation of embryos of angiosperms. He did not succeed in growing embryos smaller than those which Hannig had used though he did show that the relatively complicated nutrient solutions used by Hannig could be replaced by simpler ones.

Arnaudov (1925) found that the sporophytes of mosses could be removed from their own gametophytes and transplanted successfully into other gametophytes either of the same species, or other species. This work apparently demonstrated the nonspecificity of the nutritive substances used by moss embryos.

The author (LaRue 1929) separated sporophytes of *Dicranum montanum* from their gametophytes and imbedded their basal ends in Benecke's agar where they grew to maturity and produced normal capsules containing spores. This work suggests a greater degree of independence of sporophytes than is ordinarily assumed.

White (1932) cultivated embryos of *Portulaca oleracea* in Uspenski's solution plus a fibrin digest. Embryos 0.12 mm. long increased in size rapidly and the largest reached a maximum length of 1.84 mm. Only liquid media were used and the embryos were unable to continue growth for more than three weeks. It is noteworthy, however, that the embryos used

¹ Papers from the Department of Botany, University of Michigan, No. 562. A part of this work was done at the University of Michigan Biological Station.

were much smaller than those grown by Hannig and Dietrich. Later White (1934) was remarkably successful in growing tomato roots for indefinite periods in liquid media, but did not succeed in inducing them to develop into complete plants.

The growth of sweet cherry embryos in artificial culture was reported by Tukey (1933) and a year later (Tukey 1934) success was reported in the growth in culture of embryos of other cultivated fruits. The embryos used in these studies were nearly mature, and attempts to grow very young embryos were not successful.

Lampe and Mills (1933) reported the growth of embryos and endosperms of maize on agar containing extracts of potato or young corn, mineral salts and dextrose. Endosperms taken from the kernels ten to twenty-five days after pollination produced callus formations on the side next to the embryo. Embryos taken from grains from ten days to fifty-five days after pollination were developed in culture and afterward grown in soil.

The work described in the present paper was begun in the summer of 1935 after the author (LaRue 1936) had discovered that small bits of the immature embryos of various species could be grown in culture and induced to form complete plants. This success in the growth of tissue cultures of higher plants so often attempted since the first trials by Haberlandt (1902) in 1898 naturally led to an effort to grow complete but very young embryos in culture by the use of the same technique. The results of this effort are given in the following pages.

THE GROWTH OF DICOTYLEDONOUS EMBRYOS

The ovaries of these species were flamed on the surface and the pericarps were cut away with a sterile knife so that the ovules could be removed to a sterile slide with flamed forceps. The ovules were then dissected and the embryos placed, without washing, on the surface of the nutrient agar. Petri dishes were used for culture media usually but sometimes the embryos were transferred to plugged culture tubes which had the advantage of greater freedom from invasion by contaminating organisms but also had the disadvantage of making it difficult to observe in detail the early stages of development of the embryos.

In species of Compositae the heads were flamed before the achenes were removed but the achenes themselves were usually not flamed.

White's solution was used as a nutrient for these cultures and was made up in four lots as follows: -

Solution A. White's solution without sugar or yeast extract.

Solution B. White's solution without sugar but with yeast extract.

Solution C. White's solution with sugar and yeast extract as used in his cultures.

Solution D. White's solution with sugar but with yeast extract omitted and with synthetic hetero-auxin² added—1 part to 20 millions.

Solutions A and B did not prove satisfactory for the growth of any of the embryos, a result which might have been expected with any embryos except those which were very large and nearly mature.

Some of the early cultures were tried with liquid media in which little growth took place. On this account the remaining trials were made with either 1% or 0.75% agar-agar added. The 0.75% seemed to be more satisfactory for the embryos, but if so little agar-agar is added any hydrolysis in sterilization may result in an agar so soft that it prevents inversion of the Petri dishes for examination of the embryos.

Lactuca canadensis L. Embryos were dissected from achenes of varying ages and grew rapidly on agar containing solution D as a nutrient. Embryos 0.5 mm. long when removed from their ovules had grown to a length of 7 mm. in 11 days. After 14 days one had a root 15 mm. long and one leaf 7 mm. long. After 25 days in culture the strongest plant had a root 34 mm. long and a leaf 20 mm. long by 5 mm. wide. Three days later the root of this plant had grown to a length of 44 mm. and the first leaf was 24 mm. long by 6 mm. wide. From this stage the plants developed secondary roots and new leaves rapidly. When they were about two months old they were potted in earth where they grew normally.

Very small embryos, about 0.1 mm. long and nearly spherical in shape were dissected out from their ovules and placed on agar. They soon doubled their original size but did not continue growth thereafter.

Taraxacum officinale Weber. Embryos of this species were dissected from their achenes when about 1 mm. long. They were placed on agar containing solution D. Probably on account of their larger size their growth was more rapid than that of the embryos of *Lactuca*, but it was not different in any other way. Very small embryos, 0.1–0.3 mm., expanded to a larger size but did not grow.

Chrysanthemum Leucanthemum L. Heads of this species were picked when the corollas of the ray florets were beginning to wither. The embryos were placed on agar with solution C as a nutrient. Another lot was placed on solution D agar. These embryos ranged from 0.5 mm. to 1 mm. in length. Embryos of all sizes were capable of growth and developed in the same way and at about the same rate as those of *Lactuca*.

As a variation from the usual technique a number of endosperms con-

² The synthetic hetero-auxin was very kindly furnished me by Prof. F. C. Went of the California Institute of Technology.

taining embryos were dissected out from their seed coats and placed on solution C agar. In two days most of the embryos had broken out of their endosperms, had turned green and were growing rapidly. It was evident that the endosperm could not prevent the growth of the embryos as hard seed coats appear to do in some species.

Solution C appeared to be as satisfactory as solution D for the growth of *Chrysanthemum* embryos.

Lycopersicon esculentum Mill. Tomato embryos proved difficult to remove from the larger ovules without injury, but in the younger ovules the seed coats were still soft enough to allow easy removal of the embryos. The embryos in these younger ovules were about 0.75 mm. long and were still uncurved. On solution D agar they grew rapidly into small normal plants. Such of the larger embryos as were removed without serious injury grew more rapidly and produced proportionately larger plants.

Coreopsis lanceolata L. The embryos of this species which were available were all rather large as compared with those grown from the other species. They varied from 3 mm. to 5 mm. in length and grew into normal seedlings on solution D agar in a few days.

Nicotiana Tabacum L. and *Bryophyllum crenatum* Baker. The ovules of both these species are very small and although the embryos removed from them were only 0.5 mm. or less in length they undoubtedly represented more mature stages of development than embryos of the same size from larger-seeded species. On solution D agar the embryos of both these species grew rapidly into normal but very tiny seedlings.

Embryos of varying sizes of a number of other dicotyledonous plants were given one or more trials without success. Among these were *Alyssum saxatile compactum*, *Plantago major*, *Plantago lanceolata*, *Malva moschata*, *Eschscholzia californica*, *Linum perenne*, *Lathyrus latifolius*, *Epilobium angustifolium*, *Asclepias syriaca*, and *Melilotus alba*. Although sufficient study of these was not made to make sure they could not be grown, at this stage of progress it appears that the choice of species has much to do with the successful growth of embryos.

THE GROWTH OF MONOCOTYLEDONOUS EMBRYOS

The methods used for securing and growing monocotyledonous embryos were practically the same as those employed for dicotyledonous embryos. The fruits were always flamed before they were opened. Ears of corn with the husks on were flamed on the outside. The husks were then removed and grains themselves were flamed after their removal from the cob before they were laid on the sterile slides for dissection. In spite of all

care contaminations were common although numbers of sterile embryos could be obtained. No washing, or other means of sterilization of the embryos was attempted because it was believed that such treatment would be most detrimental to the delicate structures.

The culture solutions used were the following:

Solution 1. White's solution with sugar but without yeast extract.

Solution 2. White's solution as used by him, containing both sugar and yeast extract.

Solution 3. White's solution with sugar but without yeast extract, for which synthetic hetero-auxin was substituted—1 part to 20 millions.

Solution 4. White's solution with sugar and yeast extract plus synthetic hetero-auxin—1 part to 20 millions.

To all the solutions 1% agar-agar was added.

Avena sativa L. Embryos of oats were dissected from grains in which the endosperms were still a watery mass. The smallest embryos were exceedingly hard to find and were less than 0.5 mm. in diameter. They had a broad button-like cotyledon and a very short sharp radicle. A mere ridge indicated the coleoptile and no sign of a bud could be seen inside this coleoptilar fold. The embryos were placed on agar containing solution 4. Small as they were these embryos grew rapidly and in three days showed the beginnings of shoots. In four days good primary roots and the beginnings of adventitious roots were seen. In ten days the coleoptiles were about 3 mm. long and the roots were from 1 to 3 mm. long. The cotyledons were no larger now than they were when first removed from the grains. At this stage contamination developed and all the embryos were lost.

Larger oat embryos varied from 1 mm. to 2 mm. in length. In the smallest of these the cotyledons were circular and in the larger ones they were elongated ovate-lanceolate in outline and much thinner than those of the smaller embryos. Coleorhizae and coleoptiles were clearly defined. A number of these embryos were placed on agar containing solution 4.

After one day on the agar root hairs were seen on the coleorhizae. In three days the longest roots were 5 mm. long and the coleoptiles were curving backward away from the cotyledons, which were about 2 mm. long. The epiblasts were clearly seen as parts of the coleorhizae and were covered with short hairs which appeared somewhat different from the root hairs on the coleorhizae lower down. In nine days the longest stem was 45 mm. and the shortest 20 mm. long. In twelve days the shoots ranged from 25 to 60 mm. in length. Numerous roots were developing and were from 2 to 6 mm. long. The plants were now set in soil and continued to grow rapidly to heights ranging from 10 to 15 cm. At this time they had

to be removed from the Biological Station to Ann Arbor and all died, apparently from being kept in the dark for three days.

It is remarkable that the cotyledons never grew at all after the embryos were planted on the agar. The smaller rounded cotyledons never changed to the ovate-lanceolate shape which the larger ones had developed before they were removed from their endosperms. All development of embryonic stages was halted at once and the embryos proceeded to develop into seedlings.

Zea mays L. By far the largest number of cultures of monocotyledonous embryos was made with Indian corn. An extensive series of embryos was

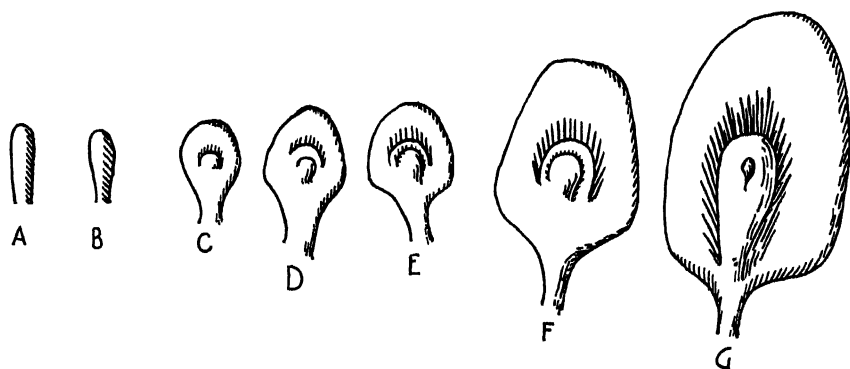


Fig. 1. Stages in the development of the embryo of *Zea mays*. The figures were prepared from camera lucida drawings of living embryos. As shown here they are magnified about 40 \times .

dissected from ears of corn ranging from the roasting ear stage down to very young ears. Trials were made with all stages from the smallest embryos which could be found under a binocular dissecting microscope using a magnification of 32 diameters up to the relatively enormous embryos found in roasting ears.

The development of the corn embryo is shown in figures 1 and 5. In all these stages the scutellum is the largest part of the embryo. In the smallest embryos shown, the suspensor and the cotyledon are the only visible parts as shown in figure 1, A, and B, and in figure 5, A. In figure 1, C, and figure 5, B, the development of a slight ridge, the coleoptile, is seen. In figure 1, D, the beginning of the plumule appears. In the series the change of the outline of the cotyledon from a rounded shape to an elongated one is shown. Unfortunately photographs of the side views of the cotyledons were not successful so that the changes in the thickness of the different parts of the cotyledons cannot be shown. These changes are

almost as great as those which are shown in figure 5. The changes shown by the developing embryos of the grasses are the most marked seen in any of the series comprising this study. For this reason the embryos of this group appear especially suitable for the study of experimental embryology.

Solutions 1, 2, 3 and 4 solidified by the addition of 1% agar-agar were used for the embryos of *Zea*. No marked difference was observed in the success of the embryos on the different solutions, but good growth and development took place on all of them.

In embryos such as are shown in figure 1, A, and B, and figure 5, A, no development was secured in culture except some increase in size and an approach to the stage shown by figure 1, B, from embryos put on agar



Fig. 2 Development of a very young embryo of *Zea mays* in culture. When placed on nutrient agar this embryo corresponded to stage C of fig. 1. A, coleoptile; B, coleorhiza; C, scutellum.

Fig. 3. Scale-like outgrowth regenerated from endosperm of *Zea mays* in culture.

at the stage shown in figure 1, A. From embryos of all the other stages growth was secured. Complete seedlings were not secured from stages like figure 1, C, but this might have occurred had not contamination overtaken the slowly developing embryos. However, the development secured was rather remarkable, for from the tiny ridge which represented the scutellum when the embryos were put on agar, coleoptiles as long as 1 mm. grew out, and coleorhizae were beginning development. The aspect of the embryos at this stage is shown in figure 2. The scutellum in most of these was exactly the same size as it was when removed from the grain, about 0.5 mm. in diameter. The only change visible was the presence of chlorophyll in this organ.

From stage D of figure 1, up to the largest embryos tested, which were from roasting ears and larger even than stage L of figure 5, complete seedlings were grown with branched roots and green leaves. Seedlings from all these stages were set in soil where they grew well for a time. The seedlings bore approximately the same relation to one another in size as the original embryos did when first placed on agar, and this difference in

size persisted until the seedlings finally succumbed to mice, slugs, and neglect.

The embryos used in these experiments were of the variety Golden Bantam. The smallest from which seedlings capable of growing in soil were developed ranged in diameter of scutellum from 0.6 mm. to 1 mm. The coleoptile and plumule were as yet scarcely more than suggested, and no sign of coleorhiza could be seen.

The rate of development of these embryos was remarkable. In one day noticeable growth took place. In two days the radicles and coleoptiles were expanding. In three days anthocyanin appeared and in six days chlorophyll was seen. The roots on the smallest embryos now averaged 2 mm. and the coleoptiles 5 mm. while the larger embryos had developed with correspondingly greater rapidity. In twelve days the coleoptiles averaged 20 mm. and the roots 10 mm. and the plants were capable of growing in earth. By the time the plants were ready to plant in soil the cotyledons were beginning to shrink and none of these organs had grown noticeably during the period of culture on agar. Neither had they undergone the changes in shape which are so marked in the embryos in their normal position in the grains. It seems that upon the transfer to agar all the embryonal stages are arrested and the embryos proceed to grow into seedlings at once.

Maize embryos without cotyledons. Cotyledons were cut away from embryos of various sizes. Embryos in which the length from tip of coleoptile to tip of coleorhiza was 1.5 mm. were the smallest that could be used without serious injury. From this size a series was prepared up to a length of 5 mm. The uninjured ones grew almost if not quite as rapidly and well as those in which the cotyledons had remained intact.

Growth of isolated cotyledons in cultures. Embryos were used the cotyledons of which were 7-7.5 mm. long and 3-4 mm. wide. The coleoptile, coleorhiza, radicle and scutellar node were scraped out from the scutellum of each embryo with a knife with a curved point. The cotyledons were then put on agar plates. The results of this trial were similar to those obtained by the writer (LaRue, 1935), with cotyledons from mature seeds.

In two days most of the cotyledons had roots ranging from 2 to 8 mm. in length. Some had only masses of tissue in the grooves from which the remainder of the embryos had been removed. At the end of four days some roots had reached a length of 20 mm. and had developed anthocyanin and root hairs.

Later several of the cotyledons developed leaflike scales but none ever formed new buds. Apparently the growth was made from fragments of the coleoptiles which were not completely removed. Perhaps the roots

were grown from primordia present also. The rapidity of their emergence would suggest this. The roots grew continually for a month and the longest one became 180 mm. long. Since no shoot had developed to feed the plants they were all discarded after one month's time.

So far as the cotyledons themselves were concerned they showed little change but did grow about 1 mm. each in length so that they finally ranged between 8 and 9 mm. in length and from 4.5 to 6 mm. in width. No obvious change in shape was noted.

In another experiment a set of embryos of yellow dent corn, much smaller than those used in the preceding test, were isolated and placed on agar with solution 1 as a nutrient. The cotyledons in these ranged from 3-4.5 mm. in length and from 2-3 mm. in breadth. The coleoptiles, radicles and scutellar nodes were removed even more carefully than in the preceding test. All of the cotyledons developed masses of tissue in the region of the connection between the scutellar node and the scutellum. Most of them developed fragmentary outgrowths of leaflike or rootlike nature but only a few produced real roots.

The cotyledons increased in size so that they finally ranged from 5-6 mm. in length, and from 3-4 mm. in width but they did not change shape to a noticeable extent. The increase in size occurred within the first three or four days and from that time on for seventeen days they made no further growth.

Growth of cotyledons on endosperm in vitro. A number of seeds of a yellow dent corn were opened and a part of the endosperm removed from each with the embryos in their natural position on the endosperms. The endosperm pieces were then placed on solution 3 in one per cent agar. In this way the embryos were kept from contact with the agar and it was hoped that the growth of roots and shoots might be delayed so that they would influence the cotyledons to a lesser degree than in the other cultures and have a chance to undergo further development themselves. The embryos used varied in stage of development from stage D to stage G as shown in figure 1. One of these was only 0.5 mm. long but produced a root 3.5 mm. long and a shoot 2.5 mm. long before succumbing to fungi. This was the best development of so small an embryo seen in any corn culture.

In spite of their position on the endosperm and their lack of contact with the agar the radicles soon developed into roots which eventually reached the agar whereupon the usual rapid growth of both roots and shoots took place. There was, however, a short delay in the beginning of growth of these organs and the cotyledons did show some effect either of this or of the contact with the endosperm, or of both.

The growth of the cotyledons was greater in most cases than in the

cotyledons described in the preceding cases. The increase in length varied from 40 to 600 per cent in the different cotyledons.

The development in shape was rather more varied than might have been expected. Some of the cotyledons increased in size with some change from stage to stage in the series shown in figure 1. However, the changes were much obscured by the growth of the coleoptiles and radicles which departed entirely from the stages shown in figure 1. Even in those cotyledons which showed a rather normal development there was an unusual increase in thickness of these organs. In a number the axis developed at right angles to the cotyledon and at the end of that organ as shown in figure 4, A.

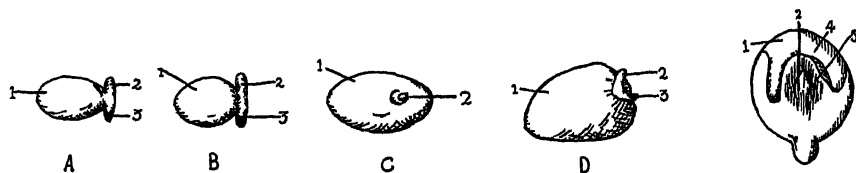


Fig 4. Development of embryos of *Zea mays* on endosperm in vitro. A and B. Embryos with unusually thick cotyledons which lie perpendicular to the axes. C and D. Stages in the development of an embryo with an abnormally swollen cotyledon. E. An embryo whose cotyledon shows two distinct parts. Legend: 1. cotyledon, 2. coleoptile, 3. coleorhiza, 4. expanded basal part of cotyledon, 5. sheathing upper part of cotyledon.

In other specimens the development was much the same as the preceding except for the greater thickness developed in the cotyledons (fig. 4, B). One interesting embryo was put on the agar in stage D, figure 1, and was only 0.5 mm. in length at the time of isolation. Hence it was very little differentiated at that time. The cotyledon increased in length from 0.5 mm. to 3 mm. and took on the shape of a football and became perched on the top of the piece of endosperm with which it was in contact. The coleoptile finally developed near one end as shown in figure 4, C, and later the radicle grew out at the end of the cotyledon (fig. 4, D). The embryo finally produced a normal root and shoot. Another cotyledon did not show so great an increase in size as the preceding but took on an even more interesting form. It showed two different regions, a lower thick flat and spreading part in contact with the endosperm and an upper thinner part which formed a sort of sheath about the coleoptile and extended downward and merged with the coleorhiza. This is shown in figure 4, E.

It is likely that the freedom from pressure of the pericarp was a factor of some importance in inducing the unusual shapes of these cotyledons. An exceedingly active fungus killed all the embryos before it was possible to

see what the ultimate shape of the cotyledons would have been when the roots and shoots had developed more completely.

Growth of excised stems and roots. In this test embryos of Golden Bantam sweet corn in the roasting ear stage were used. The shoots of the embryos were cut off in the scutellar nodes and the radicles were severed at the same point. The excised pieces, which averaged 2.5 mm. in length, were put on agar made up with each of the nutrient solutions 1, 2, 3 and 4. Whole embryos of the same age and size were cultured on the same solutions as controls.

The shoots grew in the same way as those attached to cotyledons but the rate of growth was not as great as in the complete embryos.

The excised radicles developed into roots which continued growth for fifteen days at which time many were contaminated with fungi and so all were discarded. They had reached an average length of 25 mm. or ten times their original length and appeared capable of further growth.

Development of isolated pieces of endosperm. The possibility of growth and regeneration of endosperm is of great interest. The endosperm is a tissue which continues growth until the maturity of the seed in many species, of which maize is one, but is used up as the embryo matures in others. If present in the mature seed it is digested and consumed by the embryo during germination. In germination the endosperm swells greatly but appears not to be able to renew growth after it has become dormant in the ripe seed, while the embryo which has been dormant also is able to renew active growth and development. The endosperm seems then to have no possibility of development into anything but a storage tissue and it shows relatively little differentiation. Many trials of endosperm from seeds of various species have been made by the writer, but with little result. In *Crinum asiaticum* Merry (1936) has shown that periderm is developed on wounded surfaces of endosperm, and Nakano (1924) has observed a similar though much less pronounced development in endosperm of the castor bean. The writer has observed the formation of small masses of callus on cut surfaces of endosperm of germinating corn grains but nothing more. Lampe and Mills (1933) reported that endosperm in their cultures formed callus on the side next to the embryos.

In the attempt to induce regeneration of the endosperm, pieces of corn endosperm were removed from ovules of various stages of development, but all from early stages in which the endosperm was a pearly white crisp tissue before the milk stage of the grain had appeared. These were placed on agar impregnated with solution 4. Most of them expanded though some did not, and at best the growth, if it were indeed true growth, did not amount to more than a 30 per cent increase in length and breadth of the

fragments. Several took on a faint greenish tinge which was probably due to chlorophyll, but none became really green. One produced several small knobs of tissue which did not continue growth.

Another specimen was of special interest. It was taken from the lower end of the grain with the embryo in place. The embryo was then removed, leaving a depression in which it had lain. The surface of this depression was quite smooth and the embryo came out clean without any adhering bit of endosperm. It did not appear possible that any fragment of the embryo was left behind. Yet after 8 days a little pad of tissue appeared in the depression where the embryo had lain. In ten days the endosperm undoubtedly contained chlorophyll and three small nubs of tissue had grown out around the bottom of the mass. The pad of tissue in the depression left by the removal of the embryo had now grown out into a little scale of one layer of cells with thicker portions around the edges as shown in figure 3.

At this time contamination appeared in the endosperm and the scale was soon too much damaged for use in determining the chromosome number of the cells. If this scale and the three tiny outgrowths at the bottom of the endosperm really did come from the endosperm itself we have in that the first record of any true regeneration of endosperm tissue of which the writer is aware. It seems very unlikely that the tissue came from any other source and it offers great hope that further trials, which will be made as soon as material is available, may lead to more extensive regeneration of endosperm tissue.

Panicum palmifolium Willd. Embryos have recently been removed from the minute ovules of *Panicum palmifolium*. On account of their very small size, embryos of stages as early as those of maize have not yet been grown, but those which have been developed have been of earlier stages than the largest maize embryos described in this paper. Their development has been comparable to that of the maize embryos. They have produced good roots and normal green shoots but the cotyledons do not continue growth.

Vallota purpurea Herb. The embryos of *Vallota purpurea* are under investigation at present. Success has been secured with embryos ranging from maturity down to a length of 0.5 mm. or less. Complete plants with roots and green shoots have been produced from all these. The smallest embryos used showed little differentiation at the time of their removal from the ovules. The most conspicuous thing observed in their differentiation is that the cotyledons do not continue their development beyond the stage reached before removal from the ovules, but from the beginning of culture in vitro they begin to wither. This is interesting because *Vallota* has a type of cotyledon quite different in shape from those of the Gramineae and a

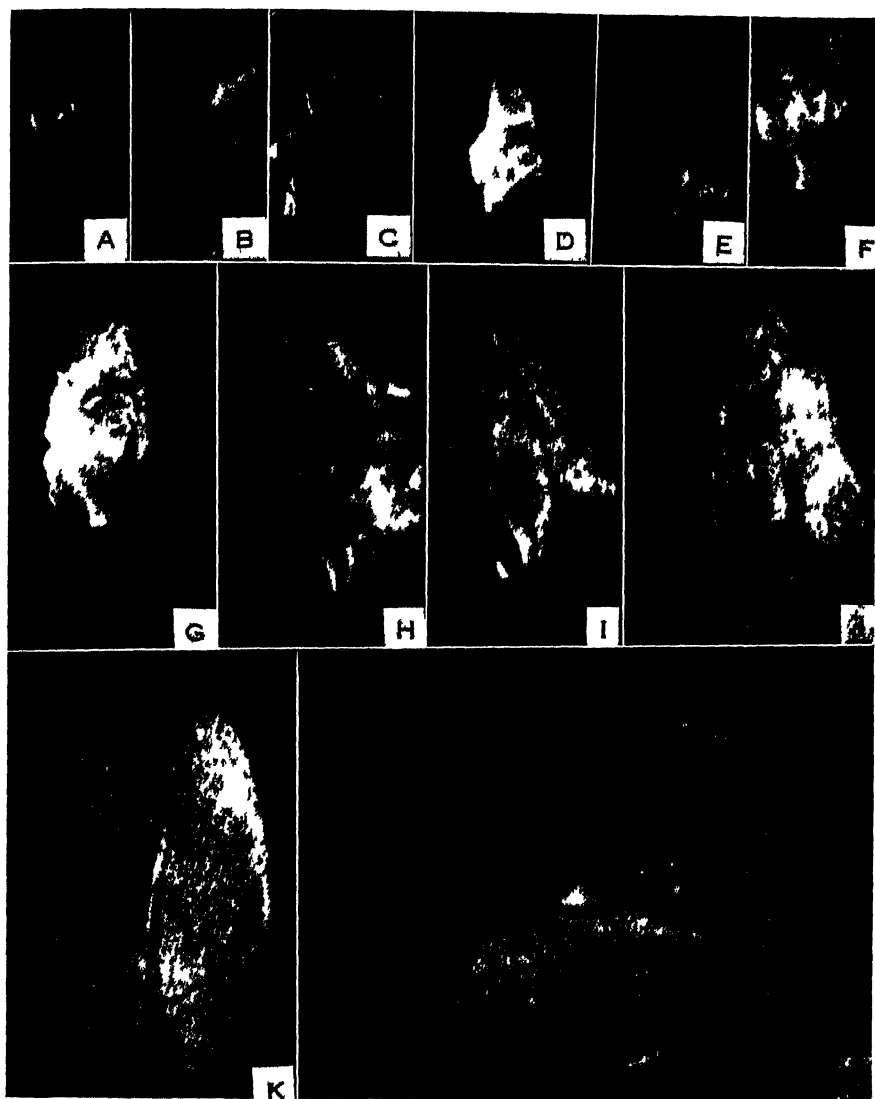


Fig 5 Stages in the development of the embryo of *Zea mays* The photographs were taken by Mr Ralph Bennett from living embryos

different type of behavior on germination. In culture these cotyledons agree with those of corn and oats, and further testify to the statement that embryos in culture do not go through the regular stages of embryonic differentiation but begin at once the production of seedling stages.

THE GROWTH OF EMBRYOS OF GYMNOSPERMS

Immature cones of *Pinus resinosa* Ait., *Thuja occidentalis* L., *Picea canadensis* (Mill.) B.S.P., *Tsuga canadensis* Carr., and *Pseudotsuga taxifolia* Britt., were flamed, after which the ovules were removed, flamed and dissected. The embryos were removed from their endosperms and placed on nutrient agar. At the time of transfer these embryos were larger than those of the angiosperms already described, since they ranged from 2 mm. to 4 mm. in length. They grew rapidly in culture and developed into normal seedlings, which were, however, much smaller than seedlings from mature seeds.

DISCUSSION

In the beginning it must be understood that this paper is the result of much work of an exploratory nature and that, necessarily, many questions have been left unanswered, while an even greater number have been raised. The most important fact seems to be that embryos of a number of species can be grown from a very immature stage into seedlings capable of continued growth, and, it is believed, to eventual maturity. In this work no seedlings have been grown to maturity but Tukey (1933, 1934) and Lampe and Mills (1933) have grown embryos to maturity from sizes smaller than those described in this paper were when they perished.

Knudson (1922) has grown seedlings of orchids from beginnings, probably smaller than any cultured by any other worker here mentioned, but they were certainly more mature since they came from ripe seeds.

The assertion of Dietrich (1924) that embryos less than one-third their full size are incapable of existence has been shown to be untrue. In fact this was shown by White (1932), who obtained growth from embryos smaller than any cultured in the present experiments, though they were not shown to be capable of *continued* existence.

Thus far it appears that though the present investigation has shown that embryos 0.5 mm. or slightly less in length can be grown successfully and without too great difficulty, those of still smaller size have not yet been brought under such control. Though the attempts at culturing them have not been sufficiently numerous to warrant a pessimistic attitude toward the possible result, it does appear to the writer that at a length of about 0.5 mm. we may have reached a new lower threshold which it will be difficult to pass.

All the successful attempts recorded in this paper were obtained with agar media. The limited growth of very small embryos reported by White was gained by the use of liquid cultures. From observation of the liquid condition of the endosperm in very young ovules it appears possible that liquid media may be best for very young embryos and that a transfer to agar media at a later stage of development might have kept White's embryos alive. So far we know so little of the conditions under which ovules develop that we cannot say with any assurance whether the embryos need aerobic or anaerobic conditions at any given stage of growth. From the rapid and normal growth of embryos in these cultures it does not appear that Dietrich's idea of the value of imbedding the embryos in agar is valid.

The development of embryos of such widely different groups of plants as gymnosperms, dicotyledons, and monocotyledons on one medium, shows that the nourishment of the embryo is not specific as the work of Stingl (1907), Arnaudov (1925) and LaRue (1929) had already indicated.

It is apparent from these studies, as Dietrich has pointed out, that no rest period is needed for embryos of many species. Dormancy in such species, is induced at a later stage, during the ripening of the seed. The question may be raised as to whether the term *after-ripening*, which connotes further development is applicable to seeds of these species.

Not much has been added to the knowledge of the morphology of the embryos of dicotyledons by these observations. Apparently the cotyledons of dicotyledonous plants fail to develop their normal size on embryos in culture. The embryos of plants of these groups show little change in shape from a size of 0.5 mm. to that of full maturity. However, the curvature of embryos is induced by the restricting influence of the ovule as Dietrich has stated. Embryos which are straight when removed from their ovules remain uncurved in their later development.

The monocotyledonous embryos undergo such striking changes in morphology during their development from a size of 0.5 mm. to maturity, that observations of such embryos in culture are much more fruitful than the study of either of the other groups. These embryos seem to offer the best material for the study of experimental embryology of plants, a subject which has long awaited the development of methods by which plant embryos could be placed under controlled conditions and kept under observation.

Dissection of maize embryos showed clearly the lateral position of the cotyledon, and thus substantiates the evidence obtained by Weatherwax (1920) from sections of the corn embryo. The cultures of *Avena* embryos showed that the epiblast belongs to the coleorhiza as Dietrich reported, and is separated from it by later expansion of the embryo.

One of the most significant differences between the morphology of embryos grown in culture from those developed in the grain is in the behavior of the cotyledon. In cultured embryos the cotyledon ceases growth as soon as the embryos are removed from the ovules, whatever the stage of development may be. However, when pieces of endosperm are placed in culture with the cotyledons undisturbed on them, the latter organs undergo considerable growth, and show strange changes in shape, of which the meaning is not clear. In one example the cotyledon developed two definite regions; a basal portion, and a sheathing upper portion. (fig. 4, E). The upper portion may perhaps be considered as an approach to the leaf sheath of the normal foliage leaf. Whether these changes are, or are not, atavistic, remains to be discovered.

The endosperm is a tissue which, if developed in culture, should be of great interest. In these cultures a few endosperm masses showed expansion and two showed small protuberances. One developed a small scale in the cleft from which the embryo had been removed (fig. 3). This appears to be the first record of an approach to real regeneration of any endosperm. If further regeneration of endosperm can be induced what will be the nature of the outgrowth?

It is obvious that the task of growing embryos in culture is only well begun but it is believed that this series of studies has materially reduced the size of the embryos which may be grown. It is important that we should attempt to grow embryos of still earlier stages of development, but with the knowledge that those of a number of species from widely differing groups can be developed in culture the way is open to many physiological studies on the requirements of the young embryo. The same knowledge makes possible the beginning of the study of the experimental embryology of plants.

SUMMARY

1. Immature embryos of *Taraxacum officinale*, *Chrysanthemum Leucanthemum*, *Lactuca canadensis*, *Coreopsis lanceolata*, *Lycopersicon esculentum*, *Nicotiana Tabacum*, and *Bryophyllum crenatum* have been grown in vitro to the seedling stage. These embryos were between 0.5 mm. and 1 mm. in length when transferred to agar media. Larger embryos were grown with proportionately greater ease.

2. Embryos of *Avena sativa* less than 1 mm. in length were grown into green seedlings. Embryos under 0.5 mm. in length were grown successfully in culture in early stages.

3. Embryos of *Zea mays*, 0.5 mm. in length, developed roots and green shoots on agar media. Slightly larger embryos were grown into plants capable of living in soil.

4. The cotyledons of corn and oats ceased growth when the embryos were transferred to agar. Corn cotyledons dissected away from coleoptiles and radicles grew little on nutrient media and did not progress into normal later stages.

5. Cotyledons of corn, removed from their ovules with portions of endosperm intact grew much more than those without endosperm, and some specimens developed into strange forms.

6. Pieces of endosperm without embryos showed slight growth on nutrient media in agar. One fragment of endosperm produced an outgrowth in the form of a flat, thin scale, the first known case of any true regeneration of endosperm.

7. Minute embryos of *Panicum palmifolium* have been grown in culture into seedlings.

8. Embryos of *Vallota purpurea* under 0.5mm. in length have developed into seedlings in culture. The cotyledons of these embryos ceased growth and withered when the embryos were placed on agar.

9. All the monocotyledonous embryos, whatever their stage of differentiation, ceased development of normal embryonic stages when transferred to agar media, and at once grew into seedlings.

10. Embryos of *Pinus resinosa*, *Thuja occidentalis*, *Picea canadensis*, *Tsuga canadensis*, and *Pseudotsuga taxifolia*, were dissected out from their endosperms and grown on agar media into small but normal seedlings.

11. The application of the methods described in this paper to various problems in physiology and experimental plant embryology is suggested.

The author wishes to express his thanks to Mr. Ralph E. Bennett for the photographs shown in figure 5.

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Some abnormalities in the development of the embryo sac of *Lilium longiflorum*

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(WITH PLATES 16-19)

The megaspore mother cell in angiosperms, as is well known, arises from a subepidermal cell of the nucellus. The development of the cell follows one of two general types, the "normal" type or the "lily" type. The first two divisions of the nucleus in both types are the meiotic divisions.

In the "normal" type at the close of the first nuclear division, a wall is formed between the nuclei; each cell again divides, giving rise to an axial row of four megaspores, separated from each other by cross walls. The three outer cells of the axial row usually disintegrate, while the remaining cell enlarges to form the embryo sac. As a result of three successive divisions the eight-nucleate stage arises. The egg and the two synergids are formed in the micropylar end of the embryo sac and the three antipodal cells are at the chalazal end. The two polar nuclei occupy the center of the embryo sac.

In the "lily" type, as has been until recently described, the egg is removed from the archesporial cell by three divisions. The first four nuclei, formed by the developing megaspore mother cell, lie free in the cytoplasm, the cross walls being absent. These four nuclei undergo mitotic division to form the eight-nucleate stage.

Peculiarities pertaining to the development of the megaspore mother cell have frequently been reported in monocotyledonous plants.

As early as 1879, Vesque observed that in *Uvularia grandiflora* an embryo sac was developed by each of two or three daughter cells of one megaspore mother cell. These developed as far as the four-nucleate stage.

Guignard (1882) figured two archesporial cells developing side by side in the hypoderm of *Ornithogalum pyrenaicum*, while Coulter and Chamberlain (1903) reported three and five archesporial cells in two preparations of *Lilium philadelphicum*.

Dixon (1895 *a* and *b*) found that without fertilization the embryo sac of *Lilium longiflorum* had a large number of nuclei present in the central portion. These were assumed to be formed by direct nuclear division from the lower polar nucleus. He also referred to peculiar forms of direct nuclear division in the endosperm of *Fritillaria imperialis*.

In her study of *Lilium Martagon*, Miss Sargent (1896 *a* and *b*) observed that in some cases the nucleus of the subepidermal cell, which is to become the megaspore mother cell, divides, thus forming twin embryo sacs. One preparation showed a double embryo sac with four spindles. Twelve chro-

mosomes were observed in the micropylar nucleus but commonly twenty-four in the chalazal one. In the four-nucleate stage, a single nucleus was observed near the micropylar end and three near the chalazal end.

Two embryo sacs in the same megaspore sac were observed by Bernard (1900) in *Lilium candidum*; by Lechmere (1910) in *Pritillaria messanensis*; by McAllister (1914) in six of the eight species of *Convallariaceae* examined.

Miss Ferguson (1907) figured two megaspore mother cells separated by a layer of somatic cells in *Lilium longiflorum*, while Miss Stiffler (1925) figured two and four megaspore mother cells occurring in one nucellus in *Cyrtanthus*. Likewise in *Veltheimia* Miss Stiffler figured a double ovule and two apparently normal megaspore mother cells side by side in one nucellus. One embryo sac contained two rows of three megasporos each. Embryo sacs of abnormal shapes also occurred.

Cooper (1934) found that in *Lilium Henryi*, after the reduction divisions were completed, three of the nuclei passed to the chalazal end of the embryo sac and one remained at the micropylar end. Then all of the nuclei divided simultaneously. The spindles of the three chalazal nuclei united and the thirty-six chromosomes became arranged on a common equatorial plate. The micropylar nucleus divided in the usual way. Thus when the divisions were completed a four-nucleate embryo sac was again formed with two $3n$ nuclei at the chalazal end and two haplod nuclei at the micropylar end. The two nuclei at the micropylar end of the embryo sac and one of the $3n$ nuclei at the chalazal end divided mitotically, the chalazal spindle having a larger number of chromosomes than the spindles of nuclei of the micropylar end. The other $3n$ nucleus divided in an "abortive manner." Thus four instead of three divisions intervened between the archesporial cell and the egg. Later Cooper (1935) made a more intensive study of this same problem. An investigation of eight species of *Lilium* yielded the same results.

METHODS

For the observations here recorded ovaries from *Lilium longiflorum* Thunb. were used. The material was collected in a greenhouse the last week in June, 1932. The few buds used were all that remained of a group of plants which bloomed about the middle of June.

The ovaries were cut into sections about a quarter of an inch in length and fixed in Flemming's medium fluid. This was done at the greenhouse. They were infiltrated in the usual way with xylol and embedded with paraffin. The sections made were from nine to twelve microns thick. The slides were stained with Flemming's triple stain (safranin, gentian-violet,

and orange G.). Occasionally light green was substituted for orange G. The results of 350 slides examined differed considerably from those which have thus far been described.

All the drawings were made with the aid of a camera lucida. The original drawings represent a magnification of $1377\times$ except figure 20 of plate 19 which represents a magnification of $635\times$. All drawings are reduced one-third in reproduction.

DISCUSSION

The ovules at first are knob-like outgrowths from the placenta. In very early stages it is difficult to determine which one of the subepidermal cells will become the megaspore mother cell. Apparently several cells are potential megaspore mother cells, but generally only one will function as such. However, not infrequently several megaspore mother cells develop simultaneously. Several instances of two cells developing in this manner occurred (fig. 1, pl. 16). These cells were either side by side as the one figured or they were in a vertical position. In one case, not figured, three megaspore mother cells are developing side by side. In all of these cases there are no signs of integuments and the general appearance of the surrounding tissues gives every indication that the cells are primary mother cells and not the result of the division of a primary cell. Single megaspore mother cells in resting condition show no abnormalities. The cytoplasm which is of a fibrillar nature is finely vacuolated. Fibrils, not always evenly distributed in the cytoplasm, appear more numerous in some places than in others. Normal spireme stages were numerous (fig. 2, pl. 16).

The two-nucleate stage is not uncommon (fig. 3, pl. 16). Sometimes the nuclei are either in a vertical position as in figure 3 or side by side. One case of incomplete nuclear division was observed in this stage (fig. 4, pl. 16). A careful examination of the preceding and following sections convinced the writer that this is not a case of overlapping nuclei, since the nuclear membrane cannot be distinguished in its entirety and the nuclear network passes freely from one nuclear portion into the other. This case is similar to those found by Steil (1919, 1933, 1935), who was the first to describe incomplete nuclear divisions and incomplete cell divisions in the sporangium of *Nephrodium hirtipes* and later in the tapetum of *Botrychium virginianum* and *Ophioglossum vulgatum*.

In *Nephrodium hirtipes* the incomplete nuclear and cell divisions occurred when the sporangium contained eight sporogenous cells. In *Botrychium virginianum* and *Ophioglossum vulgatum*, binucleate and quadrinucleate cells as well as incomplete nuclear and cell divisions were observed in the tapetum when the nuclei of the spore mother cells were in the resting

condition. Steil attributed the binucleate and quadrinucleate cells either to the failure of the second spindle to develop or to the dissolution of the second spindle and cell plate which may have formed. The incomplete divisions he attributed to probable enzyme reaction.

Incomplete nuclear divisions were also described by Roever (1935) as occurring in the tapetum of *Hosta caerulea*. The nuclei resulting from incomplete division were connected by a chromatin bridge. He figured and described a fusion occurring between the nuclei of adjacent cells; these phenomena, however, appear to be incomplete nuclear and incomplete cell division.

Figure 5 of plate 16 illustrates lagging chromosomes which probably never reach the poles. As a result incomplete nuclear division occurs.

The formation of a weak partial cell plate across the embryo sac is not uncommon (fig. 6, pl. 16; figs. 7, 8, and 9, pl. 17). That these are not merely striations in the cytoplasm is indicated in some cases by the uneven density of the cytoplasm in the two divisions (figs. 8 and 9, pl. 17). Remains of the spindle at the extremities of the partial plate are still visible in figure 6 of plate 16.

Definite partial plates with split membranes, extending vertically or obliquely across the interior of the cell but not terminated by the cell wall, were observed (fig. 12, pl. 17). The nuclei appear to be normal and in resting condition. In one case only are they shown undergoing division (fig. 10, pl. 17). The chromosomes cannot be counted with accuracy in both nuclei since they are not lying in the same plane. The number, however, is close to twenty-four, thus indicating that this is not a reduction division.

Incomplete cell divisions appearing as clefts made in the cell, similar to those figured by Steil (1935) occurred frequently (fig. 11, pl. 17).

Other irregularities are twin embryo sacs resulting from the division of the primary megaspore mother cell (figs. 14 and 15, pl. 18). The nuclei of cells thus formed sometimes undergo an unequal division. Figure 15 of plate 18 illustrates another case of incomplete nuclear division in the embryo sac to the right. One case of a triplet embryo sac not figured was observed.

Embryo sacs with three and five nuclei occurred rather frequently (fig. 16, pl. 18). Two-nucleate stages with nuclei of unequal sizes were common (fig. 17, pl. 18).

In figure 13 of plate 18 the primary megaspore mother cell divided and the result is a two-celled embryo sac. In one of these cells the nucleus is passing into synapsis; in the other the secondary megaspore mother cell has completed another division, thus forming a two-nucleate embryo sac. Integuments and surrounding cells indicate that these are older tissues and

therefore the embryo sacs are not the result of two primary megaspore mother cells developing simultaneously. Attached to this same funiculus is another megaspore sac the megaspore mother cell of which is in the spireme stage. This second embryo sac is much smaller than the one figured.

Two rows of three megaspore mother cells each were observed in one embryo sac (fig. 18, pl. 19). All of the nuclei are in the resting stage. One nucleus lies at a lower plane; consequently only the upper portion is figured. Only portions of the chromatin thread are visible.

A four-nucate stage showing incomplete cell divisions was observed (fig. 19, pl. 19).

Two megaspore sacs attached to one funiculus were frequently found (fig. 20, pl. 19). These grew either somewhat parallel or at right angles to each other. In figure 20 of plate 19 the nucleus of one embryo sac is in synapsis, while in the other there are two megaspore mother cells lying side by side.

SUMMARY

1. The megaspore mother cell of *Lilium longiflorum* develops from a subepidermal cell of the nucellus.

2. Several megaspore mother cells may develop simultaneously.

3. Twin embryo sacs may be formed by division of the megaspore mother cell.

4. Two megaspore sacs separated by vegetative tissue may be attached to a common funiculus.

5. Incomplete nuclear and cell division may occur in the course of the development of the embryo sac.

6. The first division of the megaspore mother cell is not always a reduction division.

7. Incomplete nuclear divisions result from the failure of chromosomes to reach the poles.

8. Unusual chemical activities may be responsible for the abnormalities described.

To Dr. William Steil, through whose helpful suggestions and criticisms this study was made possible, the writer wishes to express her deepest appreciation.

MARQUETTE UNIVERSITY,
MILWAUKEE, WISCONSIN

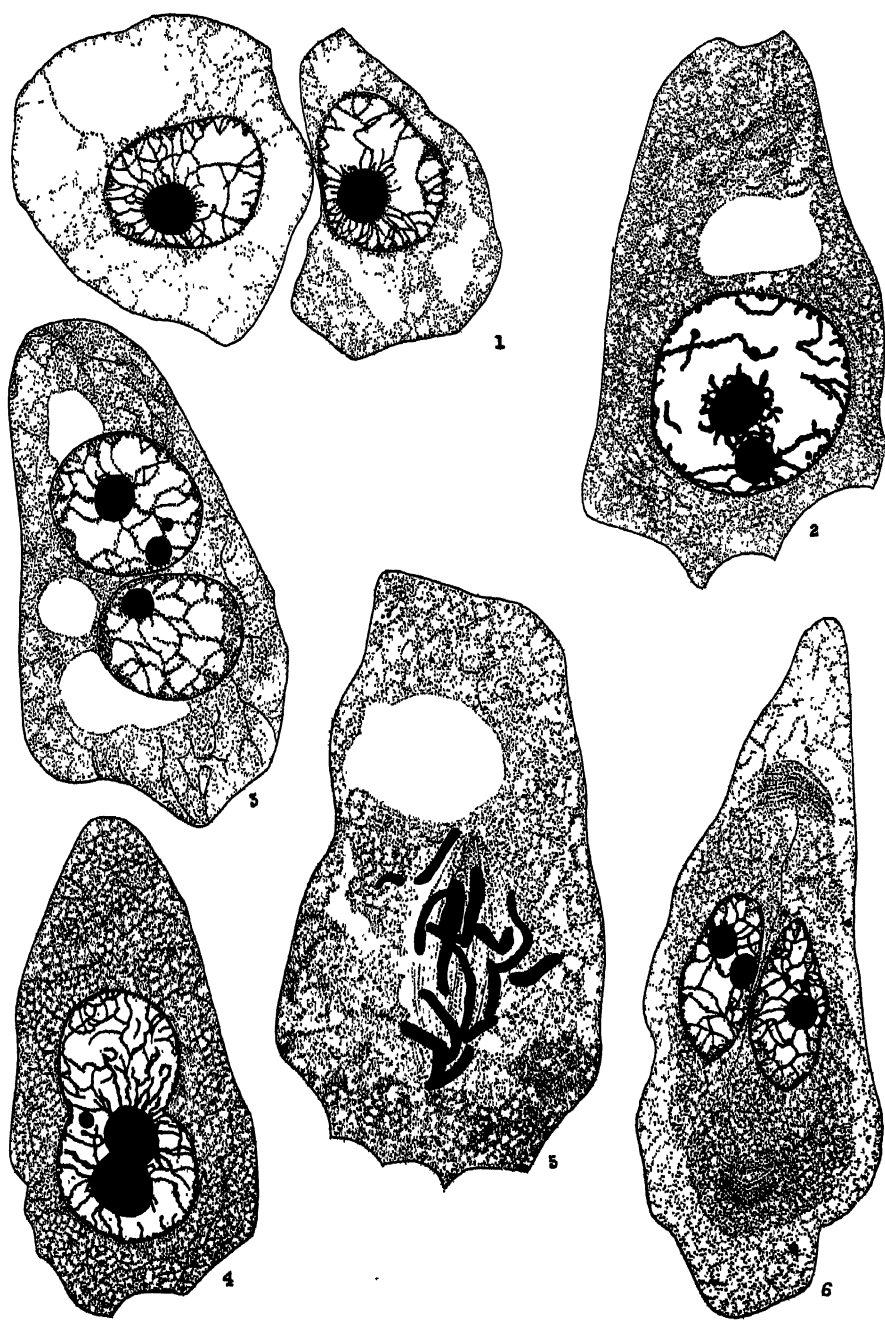
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Explanation of plate 16

- Fig. 1. Two megaspore mother cells developing simultaneously.
- Fig. 2. Megaspore mother nucleus in spireme stage.
- Fig. 3. Two-nucleate stage.
- Fig. 4. Incomplete nuclear division.
- Fig. 5. Anaphase stage of the first division showing lagging chromosomes.
- Fig. 6. Two-nucleate stage with partial plate and remains of the spindle at the extremities of the plate.



KIRCH: EMBRYO SAC OF LILIUM

Explanation of plate 17

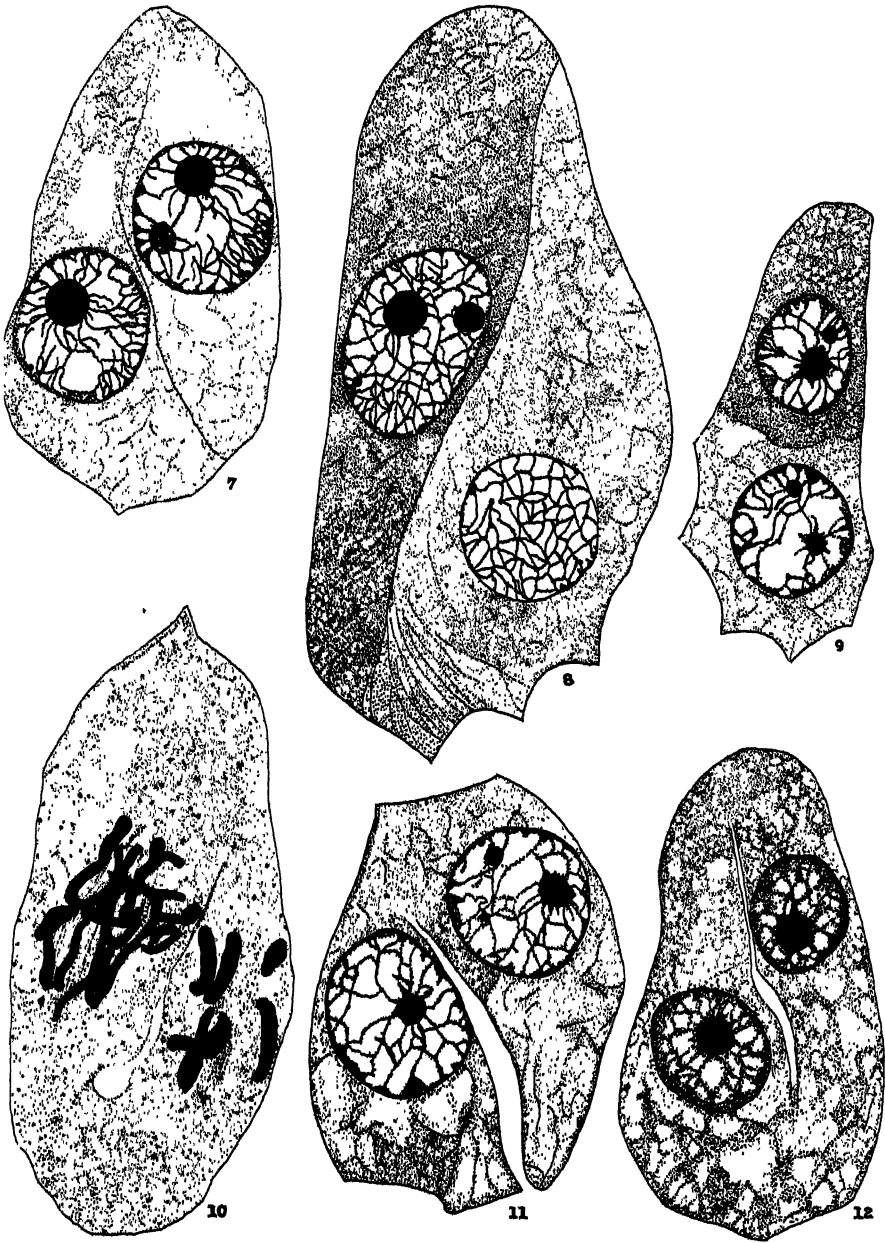
Fig. 7. Weak plate formation.

Figs. 8 and 9. Weak plate formation with cytoplasm denser in one section.

Fig. 10. Anaphase stage of second division.

Fig. 11. Incomplete cell division.

Fig. 12. Partial plate with split membranc.



KIRCH: EMBRYO SAC OF LILIUM

Explanation of plate 18

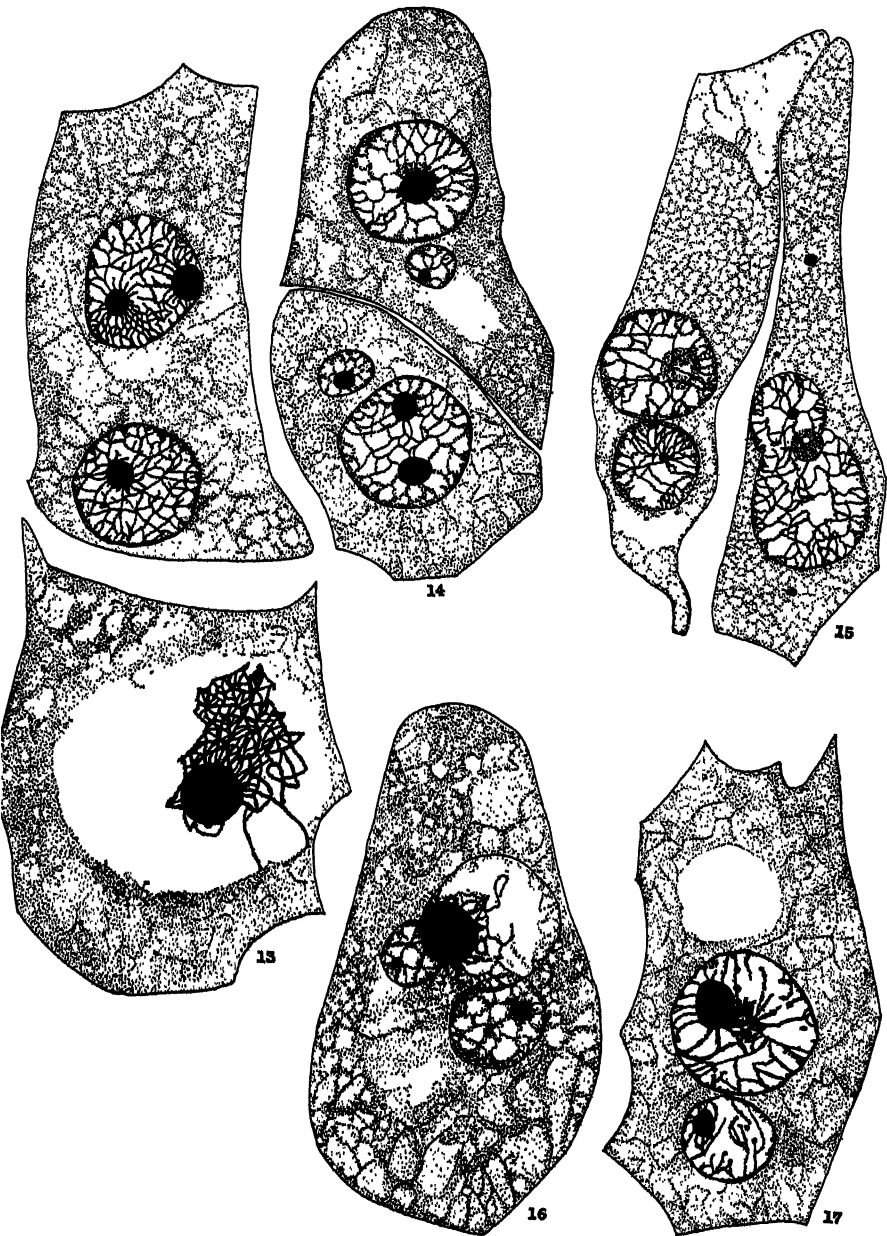
Fig. 13. Twin embryo sacs. Nucleus in lower sac is passing into synapsis. Upper sac is in two-nucleate stage.

Fig. 14. Twin embryo sacs with nuclei of uneven sizes.

Fig. 15. Twin embryo sacs. Incomplete nuclear division in the one to the right.

Fig. 16. Embryo sac with three nuclei.

Fig. 17. Embryo sac with two nuclei of unequal sizes.



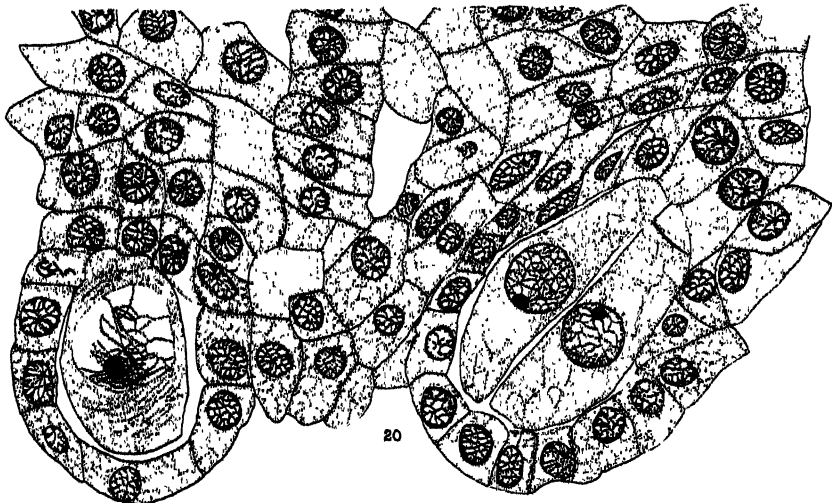
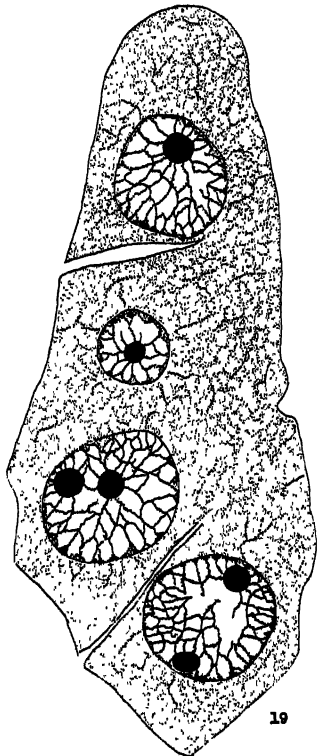
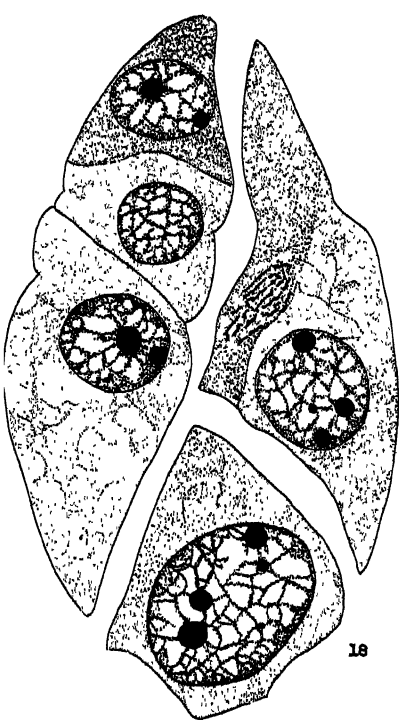
KIRCH: EMBRYO SAC OF LILIAM

Explanation of plate 19

Fig. 18. Two rows of three megaspore mother cells each.

Fig. 19. Four-nucleate stage with incomplete cell divisions.

Fig. 20. Two embryo sacs attached to a common funiculus.



KIRCH: EMBRYO SAC OF LILIUM

Revision of the *Euphorbia polycarpa* group of the Southwestern United States and adjacent Mexico; a preliminary treatment

LOUIS C. WHEELER
(WITH THREE FIGURES)

The studies on which this paper is based were carried on at the Herbarium of Pomona College under the direction of Dr. Philip A. Munz to whom I am indebted for help and guidance.

Besides expressing appreciation to Dr. Munz for his help, the writer expresses gratitude to Dr. W. L. Jepson for the loan of a critical type, to Dr. Aven Nelson for the gift of a fragment of a type, and to Dr. Ivan M. Johnston, Harvard University, Miss Ruth Sanderson, Librarian at Gray Herbarium, and Mr. Joseph A. Ewan, University of California at Berkeley, for looking up references. I am indebted to my wife Leota Wheeler for assistance in preparation of the manuscript for publication. Appreciation is expressed to the curators of the following herbaria for their kindness in loaning material:

California Academy of Sciences (CA)
University of California at Berkeley (C)
University of California at Los Angeles (UCLA)
Rancho Santa Ana Botanic Garden (RS)
Field Museum (F)
Pomona College (P)
Santa Barbara Museum of Natural History (SB)
Gray Herbarium of Harvard University (G)
Dudley Herbarium of Stanford University (D)
Herbarium of Frank W. Peirson, Altadena, Calif. (Peir)
Herbarium of Louis C. Wheeler (W)

The abbreviations given are those used in citing specimens.

LIMITATIONS OF THE GROUP

Of the section *Anisophyllum* of the genus *Euphorbia* all the entire-leaved non-shrubby species occurring in California and Lower California are intended to be included. For the rest of the arid southwestern United States which comprises Arizona, New Mexico, and Texas west of the 99th meridian, and for the bordering states of Mexico, certain groups are omitted:

1. The group with often at least moderately wide leaves, usually discoid glands, ovoid or rounded-triangular seeds, and usually annual duration, which includes *Euphorbia flagelliformis* Engelm., *Geyeri* Engelm., *polygonifolia* L., *polyclada* Boiss., *petaloidea* Engelm., and perhaps others.
2. The group with mostly linear leaves, mostly annual duration, and mostly erect habit, which includes *E. florida* Engelm., *Wrightii* T. & G.,

gracillima S. Wats., *angusta* Engelm., *zygophylloides* Boiss., and perhaps others.

The inclusion of any species in the above list does not necessarily mean that it occurs within the area under consideration. Finally, no species is here treated which does not occur in the arid southwestern United States, as above defined, or in Lower California.

HISTORY OF WORK ON THE SECTION ANISOPHYLLUM

The men who have been concerned mainly with the species treated in this paper are few. Boissier in De Candolle's *Prodromus* 15² treated all the then (1862) known species of *Euphorbia*. The species are keyed to groups of several species each by the characters which, for the most part, seem to be the least reliable, viz., duration of the plant and character of the surface of the seed. Boissier also published *Icones Euphorbiarum* in 1866. This work is very valuable in that the involucre is portrayed spread open thereby showing diagnostic characters. Engelmann described many of the new species found by the various exploring expeditions in the southwestern United States and adjacent Mexico. Millspaugh described many new species and transferred many names but did scarcely any revisional work.

HISTORY OF THE SECTION ANISOPHYLLUM

Anisophyllum as a genus: Haworth, Syn. Pl. Succ., 159. 1812, not Jacq., Select. Am., 283. 1763. As a section: Roeser in Duby, Bot. Gall. 1:412. 1828. *Chamaesyce* as a genus: S. F. Gray, Nat. Arr. Brit. Pl. 2:26. 1821. As a section: Reichb., Fl. Exc., 755. 1832. As a subsection: Boissier in DC. Prod. 15²: 27. 1862.

It is only by inference that the genus *Anisophyllum* Haworth is recognized as identical with the section *Anisophyllum*, for Roeser did not refer to Haworth's genus.

As to whether the genus *Euphorbia* should be separated into segregate genera I am not prepared to say at present.

MORPHOLOGY OF THE FLOWER

The involucre of *Euphorbia* is here considered to be a compound inflorescence rather than a simple flower. A good treatment of the anatomy and morphology of the inflorescence of *Euphorbia* is that by Dr. J. M. Haber, Ann. Bot. 39: 657-707. 1925.

EXPLANATION OF TERMS

The lower or ventral side of the stem is the side next to the ground in prostrate species. In species which are erect the morphologically upper

side can be recognized by the fact that when the leaves are inequilateral the long side of the leaf is on the upper side of the stem if the plane of the leaf is turned at right angles to the stem axis rather than parallel to it as it often lies. If the leaves are equilateral the stem rarely has differentiated sides. It is important in some cases to recognize the upper (dorsal) and the lower (ventral) sides of the stem as the stipules on one side may be united and those on the other distinct. The stipules on the lower side of the stem are more often united than those on the upper side and those toward the apex than those below. Normally there are four *glands*. These are borne on *stipes*. The glands lying next to the sinus are often larger and are here called the *proximal* glands when necessary to distinguish them from the other two or *distal* glands which are often smaller. The *fifth* gland is the rudiment of the gland which would make the involucre symmetrical. The *lobes* are the processes alternating with the glands. The *sinus* is the interval in the involucre which the fifth gland partially occupies. It is said to be *depressed* if its lower edge is below the lower edge of the interval between the lobes and glands. The staminate pedicels, here called *andropeds*, are in five groups here called *fascicles*. As each androped bears only a single stamen the two are equal in number. Each *fascicle* is opposite one of the lobes and consists of a double row of andropeds. There is a row of *bracteoles* on either side of the fascicle. Primitively there is a bracteole for each androped. The number of andropeds in some cases is, by reduction, fewer than the number of bracteoles. Usually, however, the bracteoles are fewer. In the process of reduction the bracteoles first unite below into a membranous partition, one on either side of each fascicle. Then adjacent partitions unite and form a single partition between adjacent fascicles. This partition (*bracteolar appendage*) is radial to the involucre and is usually united to it at the outer edge. The andropeds never unite and abortive ones do not seem to occur except perhaps pathologically. The pistillate pedicel, here termed *gynoped*, is usually exerted at maturity and reflexed into the sinus. The seeds are said to be *quadrangular* when they have four distinct faces here called *facets*. The *back* of the seed is opposite the raphe. The *radial direction* in the seed is the direction in which a radius of the capsule would traverse the seed, i.e., from the raphe to the back at right angles to the longitudinal axis. The *tangential direction* is at right angles to, and in the same plane as, the radial direction. In some cases the facets have transverse ridges which are said to *include* the angles, meaning that the ridges pass through the angles so that the angles have hills and valleys in silhouette. Deposited on the testa of the seed is a coat gelatinous when wet and chalky white when dry. The coat, when sufficiently thick, obscures the usually brown color of the underlying testa.

USEFUL CHARACTERS

The standard characters of annual or perennial duration and rough or smooth seeds are poor for the separation of the species. Nearly all the species in the section *Anisophyllum* bloom the first year. In the same species seeds may vary from quite smooth to at least rugulose. The presence or absence of the appendages (of the glands) must be used with great discretion for though it is constant with some species, it is extremely variable in most. The shape of the glands and seeds, the number of andropeds, the presence or absence of the fifth gland, the extent of the sinus depression, and the type of stipules and hairs are useful characters for specific segregation.

KEY TO SPECIES

- 1a. Glands discoid (circular) or radially elongate, without appendages (or with narrow appendages in *Euphorbia ocellata* var. *Rattanii*).....2
- 1b. Glands transversely (tangentially) elongate, rarely totally without appendages.6
- 2a. Andropeds (staminate pedicels each bearing one stamen) more than 10; upper stipules distinct.....3
- 2b. Andropeds fewer than 10; plants somewhat (at least the stipules) pubescent and the upper (dorsal) stipules united, or plants glabrous and stems viscid and with adhering sand grains.5
- 3a. Glands radially elongate; seeds smoothly rounded on back, face nearly flat2. *E. cremica*
- 3b. Glands strictly discoid; seeds quadrangular or ovoid.....4
- 4a. Seeds quadrangular, ca. $\frac{1}{2}$ longer than thick; leaves mostly less than 4 mm. long4. *E. Parishii*
- 4b. Seeds ovoid, or, if somewhat quadrangular, not more than $\frac{1}{2}$ longer than thick; leaves mostly over 4 mm. long1. *E. ocellata*
- 5a. Upper stipules united, pubescent; stems not viscid; seeds quadrangular.....13. *E. micromera*
- 5b. Upper stipules distinct, glabrous; stems viscid, with adhering sand grains; seeds ovoid.....3. *E. incerta*
- 6a. Stipules distinct or at least not united to form a white membranous scale.....7
- 6b. Stipules united into a white, glabrous, membranous scale.....25
- 7a. Andropeds 10 or fewer.....8
- 7b. Andropeds more than 10.....12
- 8a. Appendages narrower than the glands or wanting; sinus slightly or not at all depressed; hairs microscopically rugulose.....9
- 8b. Appendages 3-4 times as wide as the glands; sinus depressed halfway to base of the involucre; hairs microscopically smooth.....11
- 9a. Glands subcircular; seeds smooth.....13. *E. micromera*
- 9b. Glands markedly tangentially elongate; seeds wrinkled or ridged.....10
- 10a. Seed facets with white farinose transverse ridges which include the angles.....12. *E. laredana*
- 10b. Seed facets with slight transverse wrinkles which do not include the angles....11. *E. petrina*
- 11a. Appendages entire or crenate; perennial; hairs mostly clavate....9. *E. arizonica*

- 11b. Appendages deeply 3-4 parted into attenuate segments; annual; hairs tapering 10. *E. scitiloba*
- 12a. Herbage glabrous or with short, straight, spreading hairs 13
- 12b. Herbage variously clothed with appressed, long and weak, or matted hairs 17
- 13a. Seed facets with transverse ridges including the angles 14
- 13b. Seed facets smooth or with faint wrinkles not including the angles 15
- 14a. Involucres ca. 1 mm. in diam.; stems filiform (0.2-0.3 mm. diam.) 7. *E. Brandegei*
- 14b. Involucres ca. 1.5 mm. in diam.; stems stouter (0.5 mm. diam. and thicker) 8. *E. bartolomaei*
- 15a. Seeds 1.75 mm. long or longer; herbage glabrous except stipules rarely hairy 22. *E. Fendleri*
- 15b. Seeds less than 1.75 mm. long; herbage glabrous to pubescent but stipules hairy, or if glabrous, leaves conspicuously dimorphic 16
- 16a. Angles of seeds prominent; perennial; general 5. *E. polycarpa*
- 16b. Angles of seeds not elevated above facets; annual; west central Lower California 6. *E. Pondii*
- 17a. Seeds cylindrical, encircled by 4-5 rounded ridges 21. *E. pediculifera*
- 17b. Seeds quadrangular 18
- 18a. Seeds 2 mm. long or longer; leaves ovate-deltoid-falcate, or ovate-lanceolate to lanceolate and long-acuminate 19
- 18b. Seeds less than 2 mm. long; leaves not as above 20
- 19a. Leaves with a slender tapering point; at least the young stems villous 15. *E. acuta*
- 19b. Leaves blunt; herbage with short appressed hairs throughout 14. *E. lata*
- 20a. Leaves of two distinct sizes and shapes; involucre congested into glomerules 16. *E. peninsularis*
- 20b. Leaves of similar size and shape throughout; involucre not borne in glomerules though somewhat congested in *E. apicata* 21
- 21a. Appendages wider than the glands and with short spreading hairs below and on the margins 20. *E. vallis-mortae*
- 21b. Appendages wide to absent, glabrous or rarely with a few hairs beneath next to the glands 22
- 22a. Seeds with a very short inflexed apical mucro; involucre congested toward the branch tips 17. *E. apicata*
- 22b. Seeds not mucronate; involucre scattered and not congested 23
- 23a. Seed facets smooth or at least not with transverse ridges including the angles 24
- 23b. Seed facets with transverse ridges which include the angles 7. *E. Brandegei*
- 24a. Appendages usually conspicuous; styles not clavate; involucre open-campanulate 18. *E. melanadenia*
- 24b. Appendages absent or very narrow; styles clavate; involucre turbinate 19. *E. cinerascens*
- 25a. Andropeds more than 12; involucre 1.5-2 mm. in diameter 23. *E. albomarginata*
- 25b. Andropeds fewer than 8; involucre ca. 1 mm. in diameter 24. *E. serpens*

TREATMENT OF SPECIES

1. EUPHORBIA OCELLATA Durand & Hilgard, Jour. Nat. Acad. Sci. ser. 2, pt. 3:46. 1855. *Chamaesyce ocellata* (Dur. & Hilg.) Millsp., Field Mus. Pub. Bot. 2:410. 1916.

Prostrate annual from a taproot; stems to 20 cm. long, often to 1.5 mm. diam., slightly longitudinally wrinkled, glabrous or pubescent, internodes 1-3

cm. long; leaves glabrous or pubescent, blades entire, ovate-deltoid-falcate, 4-10 mm. long, apex blunt or mucronulate, base oblique, midrib elevated beneath and lateral veins prominent, margin revolute; or broadly lanceolate, 7-15 mm. long, acuminate, base obtuse and only slightly oblique, midrib not elevated below and lateral veins mostly obscure, margin plane; petioles 1.5-2 mm. long, amplexicaul on lower side of stem; stipules distinct or lower slightly united at the base toward the stem tips, filiform or broader, entire or parted, glabrous or pubescent, 1-1.3 mm. long; peduncles stout, 2-4 mm. long, glabrous or pubescent; involucre solitary in the axils, turbinate to campanulate, 1.5-2 mm. diam., five-lobed especially in late season, glabrous or pubescent without, pubescent above within; lobes broadly deltoid, pubescent on inner side or both sides and opaque throughout or glabrous and hyaline above, variously toothed or nearly entire, equaling the glands; glands discoid or slightly radially elongate, 0.5-0.75 mm. diam., yellowish or reddish, on short stout stipes which are glabrous or pubescent without and pubescent within; fifth gland linear, equaling the glands; glands exappendiculate or rarely with narrow white appendages; bracteoles nearly equaling the glands, in 5 groups opposite the glands, more or less united below and adnate to the involucre, ca. 5-10 per group, tips heavily or sparsely beset with short stout hairs; andropeds 8-13 per fascicle, 40-60 per involucre, 1.75-2 mm. long, glabrous, barely equaling or mostly shorter than the glands; gynoped glabrous or with short hairs above, long-exserted and usually reflexed at maturity; ovary three-angled, glabrous or pubescent; style ca. 0.5 mm. long, parted to the middle, glabrous throughout or pubescent below, divisions terete; capsules strongly three-lobed, ca. 2.5 mm. diam. and 2 mm. long, glabrous or with short spreading hairs, carpels rounded on the back and mostly with a very low channeled ridge on the back; seeds ovoid, with lateral angles barely visible or wanting, or turgidly quadrangular and ovate-acute radially, 0.9-1 mm. diam., 1.3-1.5 mm. long, smooth to rugose, white with a microreticulate coat, gelatinous when moistened; capsule axis breaking in the middle upon dehiscence of the capsule.

KEY TO VARIETIES

Herbage glabrous

Leaves ovate-lanceolate, not at all or very slightly falcate, acuminate, usually without evident lateral veins; seeds always smooth.....1c. var. *arenicola*

Leaves ovate-deltoid-falcate, blunt or mucronulate, lateral veins evident below; seeds often rugulose or rugose.....1a. var. *typica*

Herbage pubescent.....1b. var. *Kallanii*

- 1a. *Euphorbia ocellata* Dur. & Hilg. var. *typica* Wheeler n. nom. *Chamaesyce sulfurea* Millsp., Field Mus. Pub. Bot. 2:405. 1916.

Glabrous except within the involucre; leaves ovate-deltoid-falcate, 4-10 mm. long, apex blunt or mucronulate, base oblique, midrib conspicuous, elevated, lateral veins evident, margin revolute; glands exappendiculate; seeds smooth to rugose, back and lateral angles visible.

Type locality: Poso ("Posé") Creek, Kern Co., Calif. Distribution: Cismontane California. Representative specimens seen: CALIFORNIA: Big Chico Creek east of Chico, Butte Co., *Heller 11140* (F, type of *Chamaesyce sulphurea* Millsp., G, D, C); Auburn, Placer Co., *Ames in 1894* (G); Pardee Dam, Calaveras Co., *Howell 8168* (F, G, CA, SB); Chinese Camp Station, Tuolumne Co., *Keck 1347* (CA, W); Agua Fria, Mariposa Co., *Congdon in 1899* (C); Stockton, San Joaquin Co., *K. Brandegee in 1907* (C); 4 mi. E Corral Hollow, Mt. Diablo, Contra Costa Co., *Brewer 853* (C, G); 6 mi. N Pinnacles P. O., San Benito Co., *Howell 8043* (P, CA, C); Alcalde, Fresno Co., *Eastwood 13560* (CA); Tulare, Tulare Co., *Michener & Bioletti in 1893* (C); 10 mi. from Jolon on road to Bradley, Monterey Co., *Howell 6540* (CA, C); San Miguel, San Luis Obispo Co., *K. Brandegee in 1912* (C); 10 mi. E Bakersfield, Kern Co., *Ferris & Duncan 2207* (D, CA); San Bernardino, San Bernardino Co., *Parish 3821* (G, CA, C).

- 1b. *EUPHORBIA OCELLATA* Dur. & Hilg. var. *RATTANII* (Wats.) Wheeler, Bull. So. Cal. Acad. Sci. 33: 107. 1934. *E. Rattanii* Wats., Proc. Am. Acad. Sci. 20: 372. 1885. *Chamaesyce Rattanii* (Wats.) Millsp., Field Mus. Pub. Bot. 2: 411. 1916.

Like variety *typica* but the herbage beset throughout with short stout hairs; upper half of the gynoped, the ovary, and styles pubescent in like manner; glands often with very narrow white appendages; seeds turgidly quad-rangular, ovate-acute radially.

Type locality: Stony Creek, Glenn Co., Calif. (As Colusa Co. included Glenn Co. at the time of Rattan's collection, Watson's placing of Stony Creek in Colusa Co. was correct at the time the species was published.) Distribution: the lower Stony Creek drainage, Glenn Co. Specimens seen: CALIFORNIA: Glenn Co.: 6 mi. E Newville, *Heller 11555* (G, F, C, D, CA); Stony Creek, 2 mi. N Orland, *Wheeler 4041 in 1935* (P, UCLA, Peir, W).

- 1c. *EUPHORBIA OCELLATA* Dur. & Hilg. var. *ARENICOLA* (Parish) Jepson, Man. Fl. Pls. Calif., 600. 1925. *E. cuspidata* Engelm. ex Parish, Erythea 7: 93. 1899, in synonymy, not *E. cuspidata* Bertol. *E. arenicola* Parish, Erythea 7: 93. 1899. *Chamaesyce arenicola* (Parish) Millsp., Field Mus. Pub. Bot. 2: 408. 1916.

Leaves ovate-lanceolate, acute, to 15 mm. long, base slightly oblique, midrib straightish, not elevated below, lateral veins mostly obscure; seeds strictly ovoid or the back and lateral angles slightly evident, very smooth.

Type locality: Camp Cadly, Mohave Desert, San Bernardino Co., Calif. Distribution: Eastern Mohave Desert, Calif., Nevada, and north-western Arizona. Specimens seen: CALIFORNIA: San Bernardino Co.:

cm. long; leaves glabrous or pubescent, blades entire, ovate-deltoid-falcate, 4-10 mm. long, apex blunt or mucronulate, base oblique, midrib elevated beneath and lateral veins prominent, margin revolute; or broadly lanceolate, 7-15 mm. long, acuminate, base obtuse and only slightly oblique, midrib not elevated below and lateral veins mostly obscure, margin plane; petioles 1.5-2 mm. long, amplexicaul on lower side of stem; stipules distinct or lower slightly united at the base toward the stem tips, filiform or broader, entire or parted, glabrous or pubescent, 1-1.3 mm. long; peduncles stout, 2-4 mm. long, glabrous or pubescent; involucre solitary in the axils, turbinate to campanulate, 1.5-2 mm. diam., five-lobed especially in late season, glabrous or pubescent without, pubescent above within; lobes broadly deltoid, pubescent on inner side or both sides and opaque throughout or glabrous and hyaline above, variously toothed or nearly entire, equaling the glands; glands discoid or slightly radially elongate, 0.5-0.75 mm. diam., yellowish or reddish, on short stout stipes which are glabrous or pubescent without and pubescent within; fifth gland linear, equaling the glands; glands exappendiculate or rarely with narrow white appendages; bracteoles nearly equaling the glands, in 5 groups opposite the glands, more or less united below and adnate to the involucre, ca. 5-10 per group, tips heavily or sparsely beset with short stout hairs; andropeds 8-13 per fascicle, 40-60 per involucre, 1.75-2 mm. long, glabrous, barely equaling or mostly shorter than the glands; gynoped glabrous or with short hairs above, long-exserted and usually reflexed at maturity; ovary three-angled, glabrous or pubescent; style ca. 0.5 mm. long, parted to the middle, glabrous throughout or pubescent below, divisions terete; capsules strongly three-lobed, ca. 2.5 mm. diam. and 2 mm. long, glabrous or with short spreading hairs, carpels rounded on the back and mostly with a very low channeled ridge on the back; seeds ovoid, with lateral angles barely visible or wanting, or turgidly quadrangular and ovate-acute radially, 0.9-1 mm. diam., 1.3-1.5 mm. long, smooth to rugose, white with a microreticulate coat, gelatinous when moistened; capsule axis breaking in the middle upon dehiscence of the capsule.

KEY TO VARIETIES

Herbage glabrous

Leaves ovate-lanceolate, not at all or very slightly falcate, acuminate, usually without evident lateral veins; seeds always smooth.....1c. var. *arenicola*

Leaves ovate-deltoid-falcate, blunt or mucronulate, lateral veins evident below; seeds often rugulose or rugose.....1a. var. *typica*

Herbage pubescent.....1b. var. *Rattanii*

1a. *Euphorbia ocellata* Dur. & Hilg. var. *typica* Wheeler n. nom. *Chamaesyce sulfurea* Millsp., Field Mus. Pub. Bot. 2:405. 1916.

Glabrous except within the involucre; leaves ovate-deltoid-falcate, 4-10 mm. long, apex blunt or mucronulate, base oblique, midrib conspicuous, elevated, lateral veins evident, margin revolute; glands exappendiculate; seeds smooth to rugose, back and lateral angles visible.

Type locality: Poso ("Posé") Creek, Kern Co., Calif. Distribution: Cismontane California. Representative specimens seen: CALIFORNIA: Big Chico Creek east of Chico, Butte Co., *Heller 11140* (F, type of *Chamaesyce sulphurea* Millsp., G, D, C); Auburn, Placer Co., *Ames in 1894* (G); Pardee Dam, Calaveras Co., *Howell 8168* (F, G, CA, SB); Chinese Camp Station, Tuolumne Co., *Keck 1347* (CA, W); Agua Fria, Mariposa Co., *Congdon in 1899* (C); Stockton, San Joaquin Co., *K. Brandegee in 1907* (C); 4 mi. E Corral Hollow, Mt. Diablo, Contra Costa Co., *Brewer 853* (C, G); 6 mi. N Pinnacles P. O., San Benito Co., *Howell 8043* (P, CA, C); Alcalde, Fresno Co., *Eastwood 13560* (CA); Tulare, Tulare Co., *Michener & Bioletti in 1893* (C); 10 mi. from Jolon on road to Bradley, Monterey Co., *Howell 6540* (CA, C); San Miguel, San Luis Obispo Co., *K. Brandegee in 1912* (C); 10 mi. E Bakersfield, Kern Co., *Ferris & Duncan 2207* (D, CA); San Bernardino, San Bernardino Co., *Parish 3821* (G, CA, C).

- 1b. *EUPHORBIA OCELLATA* Dur. & Hilg. var. *RATTANII* (Wats.) Wheeler, Bull. So. Cal. Acad. Sci. **33**: 107. 1934. *E. Rattanii* Wats., Proc. Am. Acad. Sci. **20**: 372. 1885. *Chamaesyce Rattanii* (Wats.) Millsp., Field Mus. Pub. Bot. **2**: 411. 1916.

Like variety *typica* but the herbage beset throughout with short stout hairs; upper half of the gynoped, the ovary, and styles pubescent in like manner; glands often with very narrow white appendages; seeds turgidly quad-rangular, ovate-acute radially.

Type locality: Stony Creek, Glenn Co., Calif. (As Colusa Co. included Glenn Co. at the time of Rattan's collection, Watson's placing of Stony Creek in Colusa Co. was correct at the time the species was published.) Distribution: the lower Stony Creek drainage, Glenn Co. Specimens seen: CALIFORNIA: Glenn Co.: 6 mi. E Newville, *Heller 11555* (G, F, C, D, CA); Stony Creek, 2 mi. N Orland, *Wheeler 4041 in 1935* (P, UCLA, Peir, W).

- 1c. *EUPHORBIA OCELLATA* Dur. & Hilg. var. *ARENICOLA* (Parish) Jepson, Man. Fl. Pls. Calif., 600. 1925. *E. cuspidata* Engelm. ex Parish, Erythea **7**: 93. 1899, in synonymy, not *E. cuspidata* Bertol. *E. arenicola* Parish, Erythea **7**: 93. 1899. *Chamaesyce arenicola* (Parish) Millsp., Field Mus. Pub. Bot. **2**: 408. 1916.

Leaves ovate-lanceolate, acute, to 15 mm. long, base slightly oblique, midrib straightish, not elevated below, lateral veins mostly obscure; seeds strictly ovoid or the back and lateral angles slightly evident, very smooth.

Type locality: Camp Cady, Mohave Desert, San Bernardino Co., Calif. Distribution: Eastern Mohave Desert, Calif., Nevada, and north-western Arizona. Specimens seen: CALIFORNIA: San Bernardino Co.:

Mohave Desert: Hinkley, *Ferris* 1334 (D); Camp Cady (Sink of the Mohave River on some labels), *S. B. & W. F. Parish* 1370 (C, F, G, D type); Desert Wells, southeastern Calif., *Purpus* 5689 in part (C); Cronise Valley, *Munz* 12003 (P); Soda Lake, *Parish* 10375 (C, F), *Cooper*, no date (G). NEVADA: Co.? : Carson Desert, *Watson* 1077 (G); no loc., *Lemmon in* 1875 (G). Wadsworth, Washoe Co., *Kennedy* 918 (C, D), *Rubber* 945 (C), *Hillman*, no date (P); Palisade, Eureka Co., *Jones in* 1881 (P). ARIZONA: Co.? no loc. nor date, *Lemmon & wife* 37 (F). Virgin River, Mohave Co., *Purpus* 6187 (C).

2. *EUPHORBIA EREMICA* Jepson, Man. Fl. Pls. Calif., 600. 1925.

Annual; stems prostrate, 1–1.5 mm. thick, slightly longitudinally wrinkled, 10–20 cm. long, very slightly glutinous, glabrous, internodes 1–3 cm. long; leaves yellowish-green, glabrous, margin entire, blades oblong, often mucronate, 5–10 mm. long, base slightly oblique, midrib evident, petioles 1.5–2.5 mm. long; stipules glabrous, 1.5–2 mm. long, with two or three divisions, distinct, or united below toward stem apex; peduncles slightly angled, as much as 5 mm. long, glabrous; involucre solitary in the axils, glabrous without, glabrous within except for a tuft of short hairs below each gland and a small fringe at the base of each lobe, turbinate, 1.5–1.75 mm. in diam.; lobes equaling the glands, glabrous except within below, deltoid-truncate, apex entire or slightly bifid; glands mostly slightly radially elongate, 1 mm. wide, facing obliquely outward, sessile, outer margin sometimes produced into two short rounded lobes, i.e., emarginate, margin lighter color than the brownish inner portion but not differentiated into an appendage; fifth gland subulate, half as long as the lobes, glabrous, sinus U-shaped, slightly depressed; bracteoles 1–1.5 mm. long, distinct, with a few short hairs above, forming a fringe of 20–25 bracteoles around the outside of each fascicle of andropeds, not adnate to the involucre; andropeds mostly 10 per fascicle, 50 per involucre, glabrous, 2 mm. long, exserted; gynoped glabrous, long-exserted and reflexed at maturity, slightly angled; ovary glabrous, scarcely lobed; carpels evidently channeled on back; styles stout, parted to the base, 0.5 mm. long; capsule rotund-ovoid, slightly three-lobed, ca. 4 mm. long, glabrous, carpels slightly ridged on back; seeds white, microreticulate, 3 mm. long, 1 mm. radially, 1.75 mm. tangentially, oblong radially, base truncate obliquely inward, apex with an inflexed mucro, back rounded, smooth, face with two smooth, flat, nearly approximate, slightly depressed facets separated by the elevated raphe; capsule axis persistent.

Type locality: Coachella Valley ("Conchilla Desert"), Riverside Co., Calif. "*Euphorbia eremica* was collected in the Conchilla Desert between Thousand Palms Cañon and Palm Springs, but much nearer the former place," fide Jepson in litt. Known only from the type collection of a single plant. Specimen seen: CALIFORNIA: Riverside Co.: Coachella Valley ("Conchilla Desert") at ca. 200 ft., *Jepson* 6074 in May 1914 (Jepson herb.).

3. *EUPHORBIA INCERTA* T. S. Brandege, Proc. Cal. Acad. Sci. II 3: 171. 1893. *Chamaesyce incerta* (Brandegee) Millsp., Field Mus. Pub. Bot. 2: 409. 1916.

Perennial from a stout taproot, herbage glabrous, yellowish-green; branching from the base, forming tufts ca. 20 cm. high and as broad, or mats up to 60 cm. across; stems as much as 3 mm. thick, glutinous as evidenced by adhering sand grains, internodes from 5 cm. long below to 5 mm. long above; leaves long-oblong, 5–10 mm. long, entire, midrib evident, base slightly oblique, base inclined to be involute on drying, petioles 1.5–2.5 mm. long; stipules glabrous, ventral united, bifid, broadly linear, ca. 1.5 mm. long, dorsal distinct, ca. 1.5 mm. long, half as wide, 4–5 parted at the apex; peduncles stout, glabrous, as much as 2.5 mm. long; involucre solitary in the axils, short turbinate, 1.5 mm. in diam., glabrous without, sparsely beset with short hairs above within; lobes deltoid, equaling or slightly exceeding glands, entire, with a few short hairs on inner face; glands discoid or some of the proximal somewhat tangentially elongate, 0.5 mm. or less diam., on short stipes which have a few short hairs on the inner face; appendages wanting; fifth gland subulate, entire, equaling the lobes, with a few short hairs on inner face, sinus slightly depressed, broadly V-shaped; bracteoles united for ca. one-third their length into a membranous sheath around the outside of the andropod fascicle, linear above, ca. 1.5 mm. long, with a few short hairs, a few of the bracteoles united for nearly their whole length to the involucre opposite the glands; andropods 1 or rarely 2 per fascicle, 5 or 6 per involucre, stout, glabrous, ca. 1.75 mm. long, included; gynopod glabrous, long-exserted at maturity, ovary glabrous, 3-lobed; styles ca. 0.3 mm. long, bifid to middle, very stout; capsule glabrous, strongly 3-lobed, 2.5 mm. long, 3 mm. diam.; seeds spherical-ovoid, 1.75 mm. long, 1.5 mm. diam., face very slightly flattened, apex often mucronulate, coat white, microreticulate, the brown testa sometimes showing through in spots making the seed mottled in appearance; capsule axis persistent.

Type locality: La Paz, Lower California. Distribution: Sinaloa, southern Lower Calif., and near-by islands. Specimens seen: MEXICO: Sinaloa: Mazatlan, *Rose, Standley & Russel 14012* (F), *T. S. Brandege in 1893* (C). LOWER CALIFORNIA: San Francisco Island, *Johnston 3944* (C, CA); La Paz, *T. S. Brandege in 1890* (C, type), *Johnston 4010* (C, CA). Maria Magdalena, Tres Marias Islands, *Mason 1800* (CA). Socorro Island, Revillagigedo Islands, *Anthony 399* (C).

4. *EUPHORBIA PARISHII* Greene, Bull. Cal. Acad. Sci. 2: 56. 1886. *Chamaesyce Parishii* (Greene) Millsp., in Parish in Carn. Inst. Wash. Pub. 193: 6. 1913. *Euphorbia patellifera* J. T. Howell, Leaflet West. Bot. 1: 53. 1933.

Perennial, forming prostrate mats 20–50 cm. across, or a low bush 15–20 cm. high; stems slightly woody below in age, slender, glabrous, internodes 5–15 mm. long; leaves mostly ovate, 2–4 mm. long, entire, glabrous, or very

rarely tomentulose beneath, base oblique, apex mucronulate, midrib evident at least in lower half of blade, petioles 0.5–1 mm. long, glabrous, amplexicaul on ventral side of stem; upper stipules distinct, mostly entire, ciliate, broadly linear, 1 mm. long, lower stipules often more or less united, ciliate, linear, 1 mm. long; peduncles up to 1 mm. long, glabrous; involucre solitary in the axils, turbinate, 1–1.2 mm. diam, glabrous without, with many short hairs within above; lobes broadly deltoid, mostly dentate, ciliate on inner face, equaling the glands; glands discoid, ca. 0.5 mm. diam., pale yellow or reddish, on stipes ca. half as wide as the gland; stipes ciliate on inner side; appendages absent; fifth gland ciliate on inner side, linear, mostly shorter than the lobes, its sinus U-shaped, not depressed; bracteoles united for half their length, forming a membranous radial appendage ca. 1.3 mm. long, adnate for half its length to the involucre opposite each gland, glabrous below, ciliate above; andropeds 8–10 per fascicle, 40–50 per involucre, glabrous, ca. 1.5 mm. long, slightly exserted at maturity; gynoped glabrous, long-exserted and usually reflexed at maturity; ovary glabrous, three-angled; styles ca. 0.5 mm. long, bifid to the middle, glabrous; capsule glabrous, sharply three-angled, oblate-spheroid, ca. 1.75 mm. long; capsule axis persistent; seeds ca. 1.5 mm. long, ca. 0.75 mm. tangentially, ca. 0.65 mm. radially, quadrangular, long-ovate in radial outline, raphe straight, truncated above slightly, back sharply angled, facets faintly wrinkled, coat white, microreticulate.

Type locality: Warm Springs, Mohave Desert, San Bernardino Co., California. Distribution: Deserts of California from Inyo Co. south to San Diego Co. Representative specimens seen: CALIFORNIA: Inyo Co.: Surprise Wash, *Parish 10216* (C, F); Panamint Valley, *Parish 10191* (C, F); Furnace Creek, Death Valley, *L. S. Rose 33421* (CA); Funeral Mts., Death Valley, *Jones in 1907* (P, D). Kern Co.: Red Rock Canyon, Mohave Desert, *Knapp in 1888* (C). San Bernardino Co.: Mohave Desert, Daggett, *K. Brandegee in 1904* (C); Warm Springs, *Parish 1384* (D, isotype of *E. Parishii*). Riverside Co.: Colorado Desert, Cottonwood Springs, *Parish 10829* (D); Mecca, *Parish 8113* (D). San Diego Co.: Palm Wash, western Colorado Desert, *Howell 3488* (F, CA type of *E. patellifera*).

5. *EUPHORBIA POLYCARPA* Benth. Bot. Voy. Sulphur, 50. 1844. *Chamaesyce polycarpa* (Benth.) Millsp., Field Mus. Pub. Bot. 2: 411. 1916.

Perennial from a taproot slender or up to 6 mm. diam., prostrate or erect, sometimes forming a low rounded bush as much as 25 cm. high; stems very slender throughout or as much as 4 mm. diam. at base, sometimes zigzag, glabrous or with short spreading hairs, internodes mostly 1–2 cm. long, often much shorter upward; leaves glabrous or more or less pubescent, blades 1–10 mm. long, more or less oblique at base, orbicular to oblong-lanceolate, thin to thick, petioles clothed as the blades, up to 1 mm. long; lower stipules united, ca. 0.5 mm. long, deltoid or rounded, ciliate or glabrous, upper stipules dis-

tinct, narrowly deltoid, ca. 0.5 mm. long, ciliate or sometimes glabrous; peduncles to 2 mm. long, glabrous or with short spreading hairs; involucre solitary in the axils, distributed along the stem or more or less congested at the branch tips, campanulate, 1–1.5 mm. in diam., glabrous or with short spreading hairs without, glabrous within except immediately below the glands, lobes narrowly deltoid to deltoid-attenuate, equaling or slightly exceeding the glands, short hairy; glands maroon, transversely oblong, 0.5–0.75 mm. long; appendages up to three times as wide as the glands or rarely reduced to a white line beneath the glands in plants in very arid situations, as long as or longer than the gland, white or reddish, entire or crenate, glabrous or with a few short hairs below on inner portion; fifth gland absent, its sinus U-shaped and not depressed, or V-shaped and slightly depressed; bracteoles forming a radial appendage opposite each gland united to the involucre on lower half, linear, tapering upward, entire; or broader, with 2–5 divisions above, short hairy above; andropeds 1–1.25 mm. long, slightly exserted, 3–5 per fascicle, 15–30 per involucre, glabrous or rarely short-hairy above; gynopeds glabrous or short-hairy above, exserted and reflexed at maturity; ovary glabrous or densely pubescent, three-lobed; style bifid, 0.3–0.5 mm. long, glabrous or short-hairy below, clavate or slender above; capsule sharply 3-angled, glabrous or pubescent, spheroid, 1.1–1.3 mm. diam.; seeds quadrangular, 1–1.25 mm. long, ovate in radial outline, 0.5 mm. radially and tangentially, apex acutish, base truncate or obtuse, angles sharp, back curved, raphe straight, micropylar area slightly truncated, facets smooth or slightly wrinkled, plane or concave, the back facets lower than the angles, i.e., slightly depressed, coat micro-reticulate, white, opaque, or so thin that the brown testa shows through.

KEY TO VARIETIES

Leaves not strikingly of two sizes.

Leaves, except the smallest, oblong-lanceolate; suffrutescent...5c. var. *carmenensis*

Leaves orbicular to ovate or oblong.

Plants with short spreading hairs, and the appendages no wider than the glands.....5b. var. *kirtella*

Plants glabrous, or if hairy, the appendages wider than the glands

Stems zigzag, not suffrutescent; leaves oblong-orbicular and mostly 5–10 mm. long.5e. var. *genueflexa*

Stems not zigzag, sometimes suffrutescent; leaves narrower and most of them shorter than above.

Suffrutescent, i.e. stems 2–3 mm. diam. below; low rounded bush5d. var. *Johnstonii*

Herbaceous, i.e. stems to 1.5 mm. diam. below; prostrate or erect, not forming a dense bush.5a. var. *typica*

Leaves strikingly of two sizes; the larger pairs 5–10 mm. long on the main stem with long (2–3 cm.) internodes; the smaller mostly less than 5 mm. long, on short branchlets with short (3–5 mm. long) internodes.

Smaller leaves elliptic-lanceolate, acute, in several pairs.5f. var. *Mejania*

Smaller leaves ovate or oblong in one or two pairs on the branchlets.....5g. var. *intermixta*

5a. *Euphorbia polycarpa* Benth. var. *typica* Wheeler n. nom.

Prostrate or erect, sometimes slightly woody at the base in arid situations; stems very slender, to sometimes 1.5 mm. diam. at base, glabrous or with spreading hairs; leaves ovate to oblong, clothed as the stems, 2–5 mm. long; stipules ciliate, the lower united, narrowly deltoid, ca. 0.5 mm. long, the upper distinct, linear; involucre solitary in the axils, sometimes slightly congested toward the branch tips; appendages half as wide as, to three times as wide as, the glands, bracteolar appendages linear and entire or broader and 2–5 parted above, gynoped and ovary and capsule glabrous or with short hairs.

Type locality: Magdalena Bay, Lower California. Distribution: California, Nevada, Arizona, Lower California, Sonora. Representative specimens seen: CALIFORNIA: Inyo Co.: Furnace Creek, Death Valley, *Parish 10038* (C). San Bernardino Co.: Needles, *Kusche in 1921* (P, CA, G); Fort Mohave, *Cooper in 1860–61* (G). Ventura Co.: Ojai, *Peckham in 1866* (G); Point Mugu, Santa Monica Mts., *Wheeler 494* (P, W), *Hoffman in 1932* (SB). Los Angeles Co.: Garapito Creek, Santa Monica Mts., *Ewan 4197* (P, C, CA); Pasadena, *Grant 3855* (P, CA). Orange Co.: Trabuco Canyon, Santa Ana Mts., *Wolf 1859* (RS, C); 5 mi. S Laguna, *Peirson 4663* (Peir, W). Riverside Co.: Arlington, *Johnston 1254* (P); Hayfields near Desert Center, Colorado Desert, *Jones 24860* (CA, G, P). San Diego Co.: San Diego, *T. S. Brandegee in 1902* (P, C, G); Yaqui Wells, Colorado Desert, *Eastwood 2766* (CA, G). NEVADA: Searchlight, Clark Co., *Parish 10269* (C). ARIZONA: Quartzsite, Yuma Co., *Jones 24878* (CA, P); Cila Bend, Maricopa Co., *Wolf 2300* (CA, G); Sabino Canyon, Santa Catalina Mts., Pima Co., *Thorner 220* (C, P). LOWER CALIFORNIA: 29 mi. SW Tia Juana, *Jones in 1925* (P); San Quentin Bay, *Palmer 604 in 1889* (CA, F); Santa Rosalia, *Jones 22618 in small part* (P); Magdalena Bay, *Hinds in 1841*, fragment of type (F), *Dr. Lung (?)*, no date nor number (C); Todos Santos, *T. S. Brandegee in 1890* (F, C), *Jones 24509* (UCLA); La Paz, *Jones 24506* (P), *Palmer 118 in 1890* (F, C), *Rose 1309* (G); Espiritu Santo Island, *Johnston 3991b* (C, CA). SONORA: Hermosillo *Jones 22736* (P), *Rose, Standley & Russell 12382* (F); San Pedro Bay, *Craig 672* (P), *Johnston 4325* (C, CA).

This variety is composed of the residue which was not distinctly separable into the other varieties. In it are included the conspicuously appendaged plants of coastal southern California even when they have the pubescence of the narrow appendaged eremic var. *hirtella*. The narrow appendaged glabrous desert plants are also included. Habit in this variety varies from prostrate to erect even in plants growing together. The specimens from San Pedro Bay, Sonora, have the involucre produced into tubes by an insect sting. The specimens from Todos Santos, Lower California, are delicate and have the appendages conspicuously toothed.

Although I have seen a fragment of the type there is still some doubt as to the exact nature of the type due to the extremely small size of the fragment. The specimens from Santa Rosalia and Magdalena Bay (type loc.), Lower California, are peculiar in their very slender, even filiform, stems and their entire tapering bracteolar appendages. A study of the type and more specimens from the southwestern coast of Lower California might result in confining var. *typica* to this entity.

Intergrades between var. *typica* and var. *hirtella* are listed under var. *hirtella*. Intermediate between var. *typica* and var. *genuflexa* is: Cerralbo Island, Lower California, *Johnston* 4022 (C, CA). Intergrading from var. *typica* to var. *Johnstonii* is: Mulege, Lower California, *Johnston* 3666 (C, CA). Intermediate between var. *typica* and var. *Mejania* is: Muertos Bay, Lower California, *Craig* 704 (P).

5b. EUPHORBIA POLYCARPA Benth. var. *HIRTELLA* Boissier in DC., Prod. 15²: 44. 1862. *Chamaesyce polycarpa* var. *hirtella* Millsp., in Parish in Carn. Inst. Wash. Pub. 193: 6. 1913. *Chamaesyce tonsita* Millsp., Field Mus. Pub. Bot. 2: 412. 1916.

Like var. *typica* but with short spreading hairs throughout and appendages narrower than the glands.

Type locality: "California," probably Colorado Desert, Calif. Distribution: Colorado Desert, California, and islands on northeastern coast of Lower California, and adjacent areas. Representative specimens seen: CALIFORNIA: Co.?: *Emory* in 1846 (F, fragment of type). San Bernardino Co.: Needles, *Parish* 9608 (G); Pass 15 mi. from Amboy, *Munz, Harwood, & Johnston* 4179 (P). Riverside Co.: Palm Springs, *Parish* 4143 (C, G) Palm Canyon, *Johnston* in 1917 (P, C); Cottonwood Springs, Colorado Desert, *Hitchcock* 12213 (P). San Diego Co.: Dos Cabezas, *Eggleston* 19800 (P). Imperial Co.: 20 mi. NE Ogilby, *Munz & Hitchcock* 12164 (W, P, C); Signal Mt., *Wolf* 2177 (RS), *Abrams* 3187 (P, G). NEVADA: Clark Co.: Bunkerville, *Jones* in 1894 (P). ARIZONA: Yuma Co.: Yuma, *Jones* in 1906 (P). MEXICO: Lower California: Banded Agate Mt., NE Lower Calif., *Fosberg* 8351 (UCLA, D); Cedros Island, *T. S. Brandegee* in 1897 (C); San Luis Gonzales Bay, *Johnston* 3330 (C, CA); San Esteban Island, *Johnston* 3169 (G, CA, C). Sonora: Willard's Point, Tiburon Island, *Johnston* 4264 (C, CA); Tepoca Bay, *Johnston* 3307 (C, CA); Guaymas, *Palmer* 632 in 1887 (C, F).

The specimens from Banded Agate Mt., northeastern Lower California have very hairy andropeds. Some other collections from adjacent California have sparsely hairy andropeds.

It is with great reluctance that I recognize this variety as distinct from var. *typica*. While it has definite geographical range with two centers, these areas are arid deserts and the development of short spreading hairs

seems to be an ecological character in response to aridity and it occurs in other closely related species, often without particular geographical correlation. I am aware that there is a considerable hiatus between the two areas of distribution but the plants from the two areas seem to differ in no essential respect.

The Cedros Island specimen is doubtfully referred here as the appendages are markedly wider than the glands and the pubescence is rather long and weak.

Intergrades between var. *hirtella* and var. *typica*, i.e. plants insufficiently hairy to belong to var. *hirtella* proper, are represented by the following collections: CALIFORNIA: 15 mi. N Baker, Mohave Desert, San Bernardino Co., *Munz 12601* (P, C). Shaver Well, Colorado Desert, Riverside Co., *Jones in 1924* (P), *Hilend 362* (UCLA). Borrego Spring, San Diego Co., *Jones in 1906* (P). 6 mi. N Laguna Dam, Imperial Co., *Munz 11943* (P, C). MEXICO: Tiburon Island, Sonora, *Johnston 3262* (C, CA).

5c. *Euphorbia polycarpa* Benth. var. *carmenensis* (Rose) Wheeler n. comb. *Euphorbia carmenensis* Rose, Con. U.S. Nat. Herb. 1: 133. 1892. *Chamaesyce carmenensis* (Rose) Millsp., Field Mus. Pub. Bot. 2: 408. 1916.

Taproot stout; glabrous throughout except on involucre lobes and bracteoles; stems rather rigid, straightish, slender; leaves oblong-lanceolate; stipules as in var. *typica*; appendages very narrow or rudimentary; bracteoles forming a single radial, entire, or rarely, divided, deltoid-attenuate appendage opposite each gland.

Type locality: Carmen Island, Lower California. Distribution: Islands on the southeastern coast of Lower California. Specimens seen: LOWER CALIFORNIA: Carmen Island, *Palmer 842 in 1890*, type collection, (F, C); Santa Cruz Island, *Johnston 3921* (C); San Diego Island, *Johnston 3925* (C). Many of the involucre are prolonged by the sting of a cecidomyid into tubular processes faintly resembling a diminutive *Cuphea* flower. This type of parasitism is, however, not confined to this variety of *Euphorbia polycarpa* as it occurs in var. *Mejania* and on the two above cited specimens of var. *typica* from San Pedro Bay, Sonora. Also indistinguishable galls are on *Euphorbia melanadenia* from Tucson, Arizona. See comment under that name.

A specimen intermediate in leaf shape and habit between var. *carmenensis* and var. *typica* is: The Isthmus, Espiritu Santo Island, Lower California, *Johnston 3977* (C, CA).

5d. *Euphorbia polycarpa* Benth. var. *Johnstonii* Wheeler n. var.

Radix 5-7 mm. crassa; planta 15-25 cm. alta, suffrutescente; caulibus infra 2-3 mm. crassis; foliis ovato-cordatis aut oblongis, 3-5 mm. longis,

subglabris; stipulis pubescentibus, inferioribus connatis, obtusis, 0.3 mm. longis, superioribus plerumque distinctis; involucris leviter pubescentibus; appendiculis quam glandulis angustioribus; appendiculis bracteolarum linearibus vel late linearibus, plerumque integris, supra dense pubescentibus.

Type locality: Monserrate Island, Lower California. Distribution: Carmen Island and Monserrate Island off east central coast of Lower California. Specimens seen: MEXICO: Lower California: Saltworks, Carmen Island, *Johnston 4148* (C, CA); Ensenada Blanca, Monserrate Island, *Johnston 3867* (CA, C type sheet #251907). This variety is named in honor of Dr. I. M. Johnston of Harvard University who collected the type.

The specimen from Carmen Island has some of the involucre produced into galls. Intermediate in habit between var. *Johnstonii* and var. *typica* is: Tortuga Island, Lower California, *Johnston 3594* (C, CA). The following specimen is anomalous in that it is suffrutescent as in var. *Johnstonii* but the involucre are congested towards the branch tips, and the upper leaves are reduced and apiculate as in var. *Mejania*: San José Del Cabo, *T. S. Brandegee in 1893* (C). I am aware that this is far removed from the range of var. *Johnstonii*.

5e. *Euphorbia polycarpa* Benth. var. *genuflexa* Wheeler n. var.

Radix crassa; plantis cum anfractu caulium herbaceis, glabris; internodiis infra 1 cm. longis, supra gradatim brevioribus; foliis oblongo-orbicularibus, 5–9 mm. longis, glabris; stipulis illis in var. *typica* similibus; involucris dispersis, cum capillis paucis porrectisque extra; appendiculis conspicuis, glandularum latioribus; bracteolis linearibus, supra dense pubescentibus.

Type locality: Miraflores, Lower California. Specimen seen: MEXICO: Lower California: Miraflores, *T. S. Brandegee 534 in 1890* (C, type sheet #110894).

Intermediate between this variety and var. *Mejania* is: San José Del Cabo, Lower California, *T. S. Brandegee in 1887* (C).

5f. *Euphorbia polycarpa* Benth. var. *Mejania* Wheeler n. var.

Caules plerumque glabri, per totum tenues, prostrati aut ascendentes; internodiis ramorum principium 2–4 cm. longis, lateralium ramorum saepe 1–3 mm. longis; foliis plerumque glabris, duarum artium: prima 5–10 mm. longa, ovato-acuminata aut ovato-lanceolata aut late-oblongolata, acuta, in ramis lateralibus cum internodiis brevibus; stipulis plerumque glabris, inferioribus connatis, superioribus distinctis; involucris plerumque terminalibus et solitariis; appendiculis multum latioribus quam glandulis; bracteolis anguste, attenuatis, deltoideis, integris, supra paucè pubescentibus.

Type locality: Todos Santos, Lower California. Distribution: southern

end of Lower California. Specimens seen: MEXICO: Lower California: Miraflores, *Jones 24512* (P, UCLA); Todos Santos, *Jones 24510* (P type sheet #152596, UCLA), *Jones 24504* (P); Todos Santos-La Paz, *T. S. Brandegee in 1890* (C); Coast, Cape Region, *T. S. Brandegee in 1893* (P, C); San José del Cabo, *T. S. Brandegee in 1899* (C), *in 1893* (P), *Purpus 544 in 1901* (C), *Jones 27515 in part* (W), *24027* (C, P), *24505* (P, UCLA).

Long cylindrical insect-parasitized involucre galls occur on the type and some other specimens.

An intergrade between this variety and var. *typica* is: Lower California, without locality, *Anthony 352* (C). Intermediate between this var. and var. *genuflexa* in habit and leaf shape is: San Felipe, Cape Region, Lower California, *T. S. Brandegee in 1893* (C).

- 5g. *Euphorbia polycarpa* Benth. var. *intermixta* (Watson) Wheeler n. comb. *Euphorbia intermixta* S. Watson, Proc. Am. Acad. 24: 74. 1889. *Chamaesyce intermixta* (Wats.) Millsp., Field Mus. Pub. Bot. 2: 409. 1916.

Plant glabrous; stems prostrate, internodes long on main branches; larger leaves 5-7 mm. long, ovate to oblong, apex obtuse, smaller leaves 2-5 mm. long, oblong or narrower, apex obtuse, in one or two pairs on the lateral branches; involucre borne at the bifurcations of the main stems and somewhat congested on the short lateral branchlets; peduncles often up to 3 mm. long; appendages two to three times wider than glands; bracteolar appendages ca. 0.2 mm. broad, with several short slender hairy divisions above.

Type locality: Guaymas, Sonora, Mexico. Distribution: Guaymas, Sonora, and San José del Cabo, Lower California. Specimens seen: MEXICO: Sonora: Guaymas, *Palmer 187 in part in 1887* (G, type). Lower California: San José del Cabo, *T. S. Brandegee in 1893* (C). This variety may amount to nothing but the only alternative to recognition is to add another apparent entity to var. *typica*. The curious geographical distribution also suggests that this may be a form occurring sporadically over a wide range.

Intermediate between this var. and var. *Mejania* in the differentiation of the inflorescence branches and the leaves on these branches is: Lower California: [San José del Cabo by inference] without loc., *Grabendörfer in 1899* (C). Resembling var. *intermixta* in foliage and var. *typica* in the scattered involucre is: Santa Rosalia, Lower California, *Jones 22618* (P). This same collection, but another sheet, was cited, in small part, under var. *typica* but that plant was very delicate in habit and quite unlike this

6. *EUPHORBIA PONDII* Millsp., Con. U.S. Nat. Herb. 1: 12. 1890. *Chamaesyce Pondii* Millsp., Field Mus. Pub. Bot. 2: 411. 1916. *Euphorbia guadalupensis* J. T. Howell, Leaf. West. Bot. 1: 51. 1933.

Prostrate annual forming rosettes 5–10 cm. across; stems glabrous, often reddish; leaf blades to 5 mm. long, glabrous, broadly ovate, with midrib apparent for about half their length, base more or less oblique, cordate to cuneate, petioles one-half to one-third blade length, ciliate on margin at least below, stipules distinct, less than 1 mm. long, long-narrow-deltoid, margin ciliate; peduncles shorter than the involucre, glabrous to short pubescent; involucre solitary in the axils, campanulate, ca. 1 mm. in diam., glabrous to closely pubescent without, glabrous within; lobes deltoid to deltoid-attenuate, ciliate on the margin, equaling or slightly exceeding the glands; glands transversely oblong or some of the distal nearly circular, to 0.5 mm. long; appendages mostly wanting but when present narrower than the gland, white, crenate; fifth gland a low hairy papilla; sinus slightly depressed; radial bracteolar appendages adnate to involucre below, narrow, ca. 0.5 mm. long, simple or with 2–3 narrow divisions above, with a few hairs; andropeds 11–15 per involucre, ca. 0.75 mm. long, glabrous; gynoped glabrous to very shortly pubescent; ovary glabrous to finely pubescent; styles deeply parted, ca. 0.4 mm. long; capsules glabrous, three-angled, 1.5 mm. long, oblate spheroid; seeds quadrangular but the angles not prominent, ovate radially, ca. 1.25 mm. long, facets somewhat convex, faintly wrinkled, coat white, microreticulate.

Type locality: "Plaza Maria," Lower California. Perhaps Santa Maria, San Sebastian Viscaïno Bay region. Distribution: middle west coast and Guadalupe Island, Lower California. Specimens seen: MEXICO: Lower California: Plaza Maria, *Lieut. C. F. Pond*, 22 May 1889 (F, type); Guadalupe Island: *Palmer 883 in 1889* (F), *789 in 1889* (F), *J. T. Howell 8331* (CA, type of *Euphorbia guadalupensis* J. T. Howell).

While it is difficult to distinguish this species from some forms of *Euphorbia polycarpa* var. *typica* it is kept as a separate species largely because of its different physiological character of strictly annual duration and limited size. There are differentiating morphological characters but they are mostly too relative to be distinctive.

7. EUPHORBIA BRANDEGEEI Millsp., Proc. Cal. Acad. Sci. II 2: 226. 1889. *Chamaesyce Brandegeei* Millsp., Field Mus. Pub. Bot. 2: 408. 1916. *Euphorbia pediculifera* var. *minor* Millsp., Proc. Cal. Acad. Sci. II 2: 227. 1889.

Prostrate annual; stems several from the base, up to 20 cm. long, but mostly shorter, filiform, i.e. ca. 0.2 mm. diam., some up to 0.5 mm. in diam. toward the base, with sparse short tomentum, partially glabrate, internodes mostly 1–2 cm. long, those of the ultimate branchlets shorter but not congested; leaf blades 1.5–2.5 mm. long, orbicular to ovate, with sparse short tomentum, petioles 0.5–0.75 mm. long, filiform, clothed as the blades; stipules rudimentary; peduncles slender, less than 1 mm. long, with slender slightly curly hairs; involucre solitary in the axils, clothed as the peduncles, open-campanu-

late, scarcely 1 mm. in diam.; lobes deltoid-attenuate, equaling the glands, hairy; glands transversely oblong, 0.3–0.5 mm. long, reddish; appendages white, glabrous, ca. 1.25 mm. long and ca. 0.75 mm. wide, margin bluntly and irregularly lobed; fifth gland a mere hairy apiculation; sinus narrow and little depressed; bracteoles forming a single radial appendage opposite each gland, with two or three divisions above, hairy above, shorter than the andropeds; andropeds ca. 12–15 per involucre, glabrous, ca. 1 mm. long, included; gynopeds glabrous below, ovary with curly white hairs, styles very slender, parted to ca. the middle, glabrous, ca. 0.5 mm. long; capsule sparsely hairy, three-angled, ovoid, ca. 1.2 mm. long; seeds quadrangular, 1 mm. long, 0.5 mm. radially and tangentially, ovate-acute radially, base truncate, facets with low transverse ridges including the angles, coat white, micro-reticulate.

Type locality: Santa Margarita Island, Magdalena Bay, Lower California. Distribution: Magdalena Bay, Lower California. Specimens seen: MEXICO: Lower California, Santa Margarita Island, *T. S. Brandegei* in 1889, type collection of *E. pediculifera* var. *minor* (F, C); Magdalena Island, *T. S. Brandegei* in 1889, type collection of *E. Brandegei* (C, D).

This species is distinguishable from *Euphorbia bartolomaei* by the more delicate habit, the more slender styles, and the smaller seeds. It has nothing to do with *Euphorbia pediculifera*.

8. *EUPHORBIA BARTOLOMAEI* Greene, Pittonia 1: 290. 1889. *Chamaesyce bartolomaei* (Greene) Millsp., Field Mus. Pub. Bot. 2: 408. 1916.

Prostrate annual; stems to 30 cm. long, few from the base, with short sparse spreading hairs, partially glabrate; leaf blades 2–5 mm. long, sparsely short-hairy, orbicular to ovate, base oblique, margin entire, petioles ca. 1 mm. long, sparsely hairy; lower stipules united, linear, ca. 0.5 mm. long, with erect hairs at the tip and few below, upper stipules distinct, ca. 0.5 mm. long, sparsely hairy; peduncles up to 1 mm. long, with few spreading hairs; involucre solitary in the axils but borne on short congested lateral branches, campanulate, ca. 1.5 mm. diam., with short spreading hairs without, glabrous within; lobes membranous, broadly subulate-obtuse, ciliate; glands transversely oblong, 0.3–0.5 mm. long, reddish; appendages glabrous, white, 1.5–2 mm. long, 0.75–1 mm. wide, symmetrical, shallowly two- or three-blunt-toothed or lobed; fifth gland nearly absent, hairy; sinus very narrow and not depressed; bracteoles forming, opposite each gland, a single radial appendage ca. two-thirds as long as the andropeds, one-third as wide as long, or much narrower, membranous, two-to-many parted above, the divisions hairy above; andropeds included, glabrous or rarely with one or two hairs above, 1.1–1.4 mm. long, 3–4 per fascicle, 15–20 per involucre; gynopeds with spreading hairs except on the lower portion, exerted and reflexed at maturity; ovary white hairy, roundly three-lobed; styles ca. 0.3 mm. long, parted nearly to the base, very short hairy except on the stigmatic surface, stigma clavate;

capsule sharply angled, ca. 1.4 mm. long, with short sparse spreading hairs; seeds quadrangular, ca. 1.3 mm. long, ca. 0.8 mm. tangentially and radially, ovate subacute radially, base truncate, facets with low irregular transverse wrinkles including the angles especially toward the apex, coat whitish, micro-reticulate.

Type locality: San Bartolomé Bay, W central coast, Lower California. Distribution: W central coast, Lower California. Specimens seen: San Bartolomé Bay, *Lieut. Pond in 1889* (F, fragment of type); Natividad Island, *T. S. Brandegee in 1897* (C), Magdalena Island, *T. S. Brandegee in 1889* (C).

This very local species is suggestive of an intermediate between the smooth-haired *Euphorbia setiloba-arizonica* group and the microrugulose-haired *polycarpa* group proper. Some of the hairs on the bracteoles of the type are microscopically smooth. All the hairs on the Brandegee specimen from Natividad Island are microrugulose.

9. EUPHORBIA ARIZONICA Engelm. in Torr., Bot. Mex. Bound., 186. 1859. *Chamaesyce arizonica* (Engelm.) Arthur, Torreyia 11: 260. 1911. *Euphorbia versicolor* Greene, Bot. Gaz. 6: 184. 1881. *Chamaesyce versicolor* (Greene) Norton, Con. U. S. Nat. Herb. 25: 345. 1925. *Euphorbia portulana* S. Wats., Proc. Am. Acad. Sci. 24: 73. 1889. *Chamaesyce portulana* (Wats.) Millsp. Field Mus. Pub. Bot. 2: 411. 1916. *Euphorbia purissimana* [published with one "s"] Millsp., Proc. Cal. Acad. Sci. II 2: 225. 1889. *Chamaesyce purissimana* [combined with two s's, a misspelling] Millsp., Field Mus. Pub. Bot. 2: 411. 1916. *Euphorbia collina* T. S. Brandegee, U. Calif. Pub. Bot. 4: 184. 1911.

Perennial from a woody taproot, erect or prostrate, sometimes forming mats; stems up to 30 cm. long, slender, with fine, spreading, mostly clavate, microscopically smooth, hairs, internodes up to 2.5 cm. long, often much shortened towards the ends of the branches; leaves often reddish, 1–10 mm. long, deltoid-ovate, ovate, ovate-oblong with oblique base, or the upper very small and oval-cuneate, mostly with fine spreading hairs at least on the lower surface, margin entire, petioles up to 1.5 mm. long, clothed as the leaves, stipules minute and often not visible, lower united, upper distinct; peduncles filiform, with fine spreading hairs, 1–4 mm. long, mostly 1–2 mm. long; involucre solitary in the axils but often congested by the shortening of the upper internodes, long-turbinate, constricted above, ca. 1.5 mm. long, 0.8 mm. diam., with sparse short spreading hairs without, glabrous within; lobes subulate, equaling the glands, entire, ciliate on the margins; glands 1.5–2 times as long as wide, 0.3–0.4 mm. long, concave, red; appendages glabrous, oval, up to 1 mm. long, white but red in age; fifth gland absent, its sinus narrowly V-shaped and depressed halfway to base of the involucre; bracteoles reduced to one sparsely hairy filiform appendage adnate below to the in-

volucre opposite each gland, two-thirds as long as the involucre or shorter; andropeds 5-10 (or rarely 12), mostly 6-7, glabrous, equaling the glands, 1.5 mm. long; gynoped glabrous, long-exserted and reflexed at maturity; ovary three-lobed, densely pubescent, styles parted to the middle, slender, glabrous, ca. 0.6 mm. long; capsule with spreading hairs, spheroid with flattened base, ca. 1.5 mm. long and diam., obtusely three-angled, axis persistent after dehiscence; seeds quadrangular, ca. 1.25 mm. long, base truncate, outline narrowly ovate radially, raphe obliquely truncated by the micropylar region, facets with low, often anastomosing, ridges which slightly include the angles, white coat very thin, the brown testa showing through.

Type locality: Sierra Yanos ("Sierra del Yanno"), Sonora. Distribution: California to Texas, Sonora and Lower California. Representative specimens seen: CALIFORNIA: Riverside Co.: Andreas Canyon, Palm Spring region, *Peirson 4256* (Peir). San Diego Co.: Palm Canyon, Borrego Valley, *Templeton 1632* (Los Angeles County Museum, P). ARIZONA: Mohave Co.: Yucca, *Jones in 1884* (P). Coconino Co.: Grand Canyon, *Lemmon in 1884* (F, D). Pinal Co.: Winkelman, *Peebles, Harrison & Kearney 5181* (UCLA). Pima Co.: Sabiño Canyon, Santa Catalina Mts., *Thornber 221* (D, P). Greenlee Co.: San Francisco Mts. near Clifton, *Greene in 1880*, type collection of *Euphorbia versicolor* Greene (F, G). NEW MEXICO: Doña Ana Co.: Peña Blanca, *Wootton in 1903* (P). TEXAS: El Paso Co.: El Paso, *Jones in 1884* (P, D). MEXICO: Lower California: Agua Verde Bay, *Johnston 3878* (CA); Purisima, *T. S. Brandegee in 1889*, type collection of *Euphorbia purisimana* Millsp. (C). Sonora: Guaymas, *Wm. Palmer 1225* (F), *E. Palmer 321 in 1887*, isotype of *E. portulana* Wats. (C), *Rose, Standley & Russell 15010* (G, F); Sierra del Yanno, *Schott in 1855*, type collection of *E. arizonica* (G, F), ("Arizona" on some copied labels at F). Durango: Cerra de San Ignacio, *Purpus 4599 in 1910* (C, type of *E. collina* T. S. Brandegee).

The specimen from Purisima, Lower California is atypical in the reduced appendages and less than average pubescence. The peculiar appearance of the plant is largely due to its dark color caused probably by slow drying. The Durango specimen is quite typical though far out of the usual range.

(to be concluded)

INDEX TO AMERICAN BOTANICAL LITERATURE

1931-1936

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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Revision of the *Euphorbia polycarpa* group of the Southwestern United States and adjacent Mexico; a preliminary treatment

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(concluded)

10. *EUPHORBIA SETILOBA* Engelm., ex Torrey, Pacif. Rail. Rep. 5: 364. 1857. *Chamaesyce setiloba* (Engelm.) Millsp., in Parish, Carn. Inst. Pub. 193: 6. 1913. *Chamaesyce setiloba* (Engelm.) Norton, Con. U. S. Nat. Herb. 25: 345. 1925. *Euphorbia floccosiuscula* Jones, Con. West. Bot. 15: 145. 1929.

Annual, with microscopically smooth tapering hairs throughout; stems slender, prostrate or perhaps rarely erect, rarely forming mats, internodes up to 2 cm. long, often much shortened toward the stem tips congesting the leaves and involucre into dense small "heads"; leaf blades 2–5 mm. long, oblong or oblong-ovate, base slightly oblique, petioles up to 1 mm. long; stipules not apparent; peduncles up to 1.5 mm. long, clothed as the herbage, filiform; involucre solitary in the axils, very shortly hairy without, glabrous within, long turbinate, constricted above, ca. 1.2 mm. long, ca. 1 mm. in diam.; lobes narrowly deltoid, entire, ciliate, equaling the glands; glands red, transversely oblong or the distal sometimes discoid, concave, 0.1–0.2 mm. long; appendages white, glabrous, ca. 1 mm. long and wide, parted into 3–5 narrow attenuate segments; fifth gland totally absent, its sinus depressed halfway to base of the involucre; bracteoles reduced to one filiform appendage adnate below to the involucre opposite each gland, with few or no hairs, free portion only ca. 0.2 mm. long; andropeds glabrous, ca. 1.2 mm. long, ca. equaling the glands, 3–7 per involucre; gynoped glabrous or with a few hairs above; ovary three-lobed, long white hairy, styles glabrous, 0.4–0.5 mm. long, parted to the base, clavate, slender; capsule long-hairy, spheroid, ca. 1.1 mm. long, sharply angled, capsule axis persistent; seeds 0.9–1 mm. long, quadrangular, sharply angled, facets with low irregular wrinkles, base truncate, ovate acutish radially, coat microreticulate, white but the brown testa showing through.

Type locality: Fort Yuma, Imperial Co., California. Distribution: southeastern California, Arizona, Lower California, Sonora, Sinaloa. Representative specimens seen: CALIFORNIA: Inyo Co.: Shepherd's Canyon, Argus Mts. *Jones in 1897* (P, F, D). San Bernardino Co.: 3 mi. N Cave Spring, Mohave Desert, *Peirson 8705* (Peir). Riverside Co.: Corn Spring, *Jones in 1926* (P); Dos Palmas, Colorado Desert, *Jaeger in 1921* (Peir); Riverside Mt., Colorado River, *Grinnell in 1910* (C). San Diego Co.: Mt. Springs, *Parish 9034* (D). Imperial Co.: *Major Thomas*, without loc. or date but probably from Fort Yuma (G, fragment of type?); 20 mi. NE Ogilby, *Munz & Hitchcock 12153* (P, C). ARIZONA: Mohave Co.: Kingman, *Braem in 1927* (D); Hackberry, *Rusby in 1883* (F, C). Coconino Co.:

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Williams Fork, *Palmer 514 in 1876* (G). Yuma Co.: Quartzsite, *Jones 24880* (UCLA, C, G, CA, P). Gila Co.: Sierra Ancha, *Harrison & Kearney 8292* (P). Pinal Co.: Apache Junction, *Gillespie 8432* (C). Pima Co.: Santa Catalina Mts, *Lemmon in 1880* (F, C), *in 1881* (C); Tucson, *Sherff in 1908* (F, C), *Jones in 1903* (P). Greenlee Co.: San Francisco Mts. near Clifton, *Greene in 1880* (F). Cochise Co.: Apache Pass, Chiracahua Mts., *Lemmon in 1881* (C). LOWER CALIFORNIA: Santa Rosalia, *Ferris 8698* (D, P), *Jones 22618 in part* (P); Purisima, *T. S. Brandegee in 1889* (F, C); Los Angeles Bay, *Palmer 629 in 1887* (G, 2 sheets, one sheet labeled Guaymas, but this is doubtless in error as Watson, Proc. Am. Acad. 24:75. 1889, in a list of plants collected by Palmer, gave this number as from Los Angeles Bay). SONORA: no loc., *Pringle in 1884* (F, G); Hermosillo, *Jones 22739* (P, type of *Euphorbia floccosiuscula* Jones), *Rose, Standley & Russell 12494* (F); Guaymas, *Palmer 185½ in 1887* (F, G). SINALOA: San Blas, *Rose, Standley & Russell in 191-* (F); Fuerte, *Rose, Standley & Russell 13540* (F).

Palmer's 185½ from Guaymas is atypical in having longer internodes, larger leaves, and less deeply cut appendages than usual.

11. *EUPHORBIA PETRINA* Wats., Proc. Am. Acad. 24: 75. 1889. *Chamaesyce petrina* (Wats.) Millsp., Field Mus. Pub. Bot. 2: 411. 1916. *Euphorbia polycarpa* Benth. var. *petrina* (Wats.) Johnston, Proc. Cal. Acad. Sci. IV 12: 1072. 1924.

Annual or perennial, prostrate, sometimes forming mats 30 cm. across; stems with fine spreading hairs, sometimes glabrate in age, internodes up to 1.5 cm. long, greatly shortened at the stem tips thereby congesting the leaves and involucre; leaves finely pubescent, blades entire, ovate, base markedly oblique-cordate, less oblique in the reduced upper leaves, 2-5 mm. long, juvenile leaves often much larger, variable in shape, subentire, petioles less than 1 mm. long; stipules minute, obscured by the pubescence of the stem; peduncles pubescent, less than 1 mm. long; involucre solitary in the axils, less than 1 mm. diam., short campanulate, cuneate to the peduncle, pubescent without, glabrous within except on the lobes, green veined opposite the lobes; lobes triangular, densely hairy, shorter than the glands; glands transversely oblong, 2-3 times longer than wide, up to 0.3 mm. long, red, mostly exapendiculate, or with very narrow white crenate appendages; fifth gland absent; sinus broadly V-shaped, slightly depressed; bracteoles reduced to one radial appendage adnate for half its length to the involucre opposite each gland, linear, parted to the middle, hairy above, ca. two-thirds as long as the andropeds; andropeds ca. 5 per involucre, glabrous, ca. 1 mm. long, barely equaling the glands; gynoped hairy above, exserted and reflexed at maturity; ovary three-angled, white hairy, styles bifid, glabrous, ca. 0.3 mm. long;

capsule glabrate on sides of the carpels, ca. 1.25 mm. diam., ca. 1 mm. long, axis persistent after dehiscence; seeds quadrangular, ca. 0.9 mm. long, ca. 0.6 mm. tangentially, ca. 0.5 mm. radially, ovate radially, base concave-truncate, facets convex, with gentle low irregular transverse ridges, white coat very thin, the brown testa showing through.

Type locality: San Pedro Martir Island, Lower California. Distribution: southern Lower California, Sonora, Sinaloa. Specimens seen: MEXICO: Lower California: San Pedro Martir ("Martin") Island, *Palmer 412 in 1887* (G type, C, F on copied label loc. is "Maleja, Lower Calif."). San Esteban, *T. S. Brandegee 39 in 1889* (F, C). Sonora: Alamos, *Rose, Standley & Russell 12900* (F). Sinaloa: Fuerte, *Rose, Standley & Russell 13453* (F); San Blas, *Jones 23313* (P, C, CA, G); Culiacan, *T. S. Brandegee in 1904* (C), *Palmer 1808 in 1891* (G).

12. EUPHORBIA LAREDANA Millsp., *Pittonia* 2: 89. 1890. *Chamaesyce laredana* (Millsp.) Small, Fl. SE U. S., 709. 1903.

Prostrate annual; plant more or less tomentose throughout; stems several, 10–20 cm. long, stout (1.5 mm. diam.) toward the base, internodes to 1 cm. long; leaf blades extremely oblique even to the small upper ones, ovate (distorted by the obliquity) 3–5 mm. long, margin entire or the large juvenile leaves with a few low discrete teeth, petioles less than 1 mm. long; stipules minute and obscured by the tomentum; peduncles ca. 0.5 mm. long; involucre solitary in the axils, tomentose without, glabrous within except above, short campanulate, cuneate to the peduncle, 1 mm. or less diam., green veined opposite the lobes; lobes deltoid, equaling or slightly exceeding the glands, hairy; glands transversely oblong, 0.2 mm. long or shorter, yellowish; appendages absent or very narrow; fifth gland absent; sinus slightly depressed and with long hairs; bracteoles reduced to one radial appendage opposite each gland, adnate to the involucre for half its length, entire to one or two-parted to the base, hairy above; andropeds 5 or fewer per involucre, glabrous, 1 mm. long, included; gynoped tomentose above, glabrous below, exerted and reflexed at maturity; ovary sharply three-angled, tomentose, styles bifid, less than 0.2 mm. long; capsule glabrate on the sides of the carpels, the backs usually persistently tomentose, sharply three-angled, 1.5 mm. long, 1.5 mm. diam; seeds sharply quadrangular, narrowly ovate radially, base concave-truncate, facets concave, with irregular white farinose transverse ridges including the angles, 1.1–1.2 mm. long, 0.5 mm. radially and tangentially; capsule axis persistent.

Type locality: Laredo, Webb Co. Texas. Distribution: Known only from the type locality. Specimens seen: TEXAS: Webb Co.: Laredo, *Pringle 2074* (F, type), *2070* (G), *Reverchon 3786* (P, G), *Pringle 3747* (C, F, P, G).

13. EUPHORBIA MICROMERA Boissier, DC. Prod. 15²: 44. 1862. *Chamaesyce micromera* (Boiss.) Wooton & Standley, Contr. U. S. Nat. Herb. 16: 144. 1913. *Euphorbia pseudoserpyllifolia* Millsp., Pittonia 2: 87. 1890. *E. pseudoserpyllifolia* forma *typica* Howell, Leaf. West. Bot. 1.52: 1933. *E. pseudoserpyllifolia* forma *villosa* Howell, Leaf. West. Bot. 1: 53. 1933. *Chamaesyce pseudoserpyllifolia* Millsp., Field Mus. Pub. Bot. 2: 411. 1916. *Euphorbia podagrica* Johnston, Univ. Calif. Pub. Bot. 7: 440. 1922.

Prostrate annual; stems glabrous or pubescent, extremely variable, one extreme very straight, thick, with thickened nodes, and internodes up to 1 cm. long, the other extreme flexuous or straightish, slender, nodes not thickened, internodes up to 2 cm. long; leaves glabrous or short pubescent, blades 2–7 mm. long, ovate and base markedly oblique in the larger, oblong and base slightly oblique in the smaller, petioles ca. 0.5 mm. long; stipules ca. 0.75 mm. long, or shorter in pubescent plants, triangular, ciliate, upper distinct, lower often united toward stem tip; peduncles glabrous or pubescent, up to 1 mm. long; involucre solitary in the axils, ca. 1 mm. in diam., very short campanulate, narrowed above, more or less cuneate to the peduncle, glabrous or pubescent without, glabrous within except the lobes, green veined opposite the lobes; lobes deltoid, equaling or slightly exceeding the glands, hairy within; glands pink or red, strictly discoid or slightly transversely elongate, especially the proximal, 0.1–0.15 mm. diam.; appendages absent; fifth gland absent; sinus broadly V-shaped, hairy, little depressed; bracteoles reduced to a solitary linear hairy appendage ca. 0.5 mm. long, adnate for most of its length to the involucre opposite the glands; andropeds mostly 5 per involucre, glabrous, included, barely 1 mm. long; gynoped glabrous throughout or short hairy above, long-exserted and usually reflexed at maturity; ovary three-angled, glabrous to pubescent, carpels slightly grooved on the back; styles bifid, glabrous, 0.1 mm. long; capsule three-angled, glabrous or glabrate, spheroid, ca. 1.3 mm. long; seeds quadrangular, 1.1–1.3 mm. long, 0.5 mm. tangentially, 0.4 mm. radially, narrowly ovate radially, angles sharp, facets smooth or with very faint wrinkles, convex, especially the front, base truncate, raphe straight or slightly concave, shortly truncate at a slight angle above, microreticulate white coat thin, with the brown of the testa showing through.

Type locality: New Mexico. Distribution: deserts of Nevada, California, Arizona, New Mexico, northern Lower California, and Coahuila. Specimens seen: NEVADA: Co.?: Gold Mt., *Purpus* 6437 in part (C, type of *Euphorbia podagrica* Jtn.). Mineral Co.: Sodaville, *Brandegge Herb. (collector?) in 1912* (C). CALIFORNIA: Inyo Co.: Owens Lake, *Purpus* 3046 (C); Darwin Mesa, *Hoffmann in 1931* (SB). Los Angeles Co.: Rosamond, *collector not stated, in 1929* (SB). Riverside Co.: Colorado Desert: Salton Bench Mark, *Wheeler* 369 (W, P, Peir); Desert Center, *Jones* 24879 (UCLA, C, CA, P in part); Cathedral City, *Howell* 6651 (CA, type

of *Euphorbia pseudoserpyllifolia* Millsp. forma *villosa* Howell). San Diego Co.: San Felipe Valley, *Hoffmann in 1929 in part* (SB). Imperial Co.: between Brawley and Salton Sea, *Parish 8301* (G, D, F "SW Brawley" on the label); Colorado River bottoms at Fort Yuma, *Parish 8307* (D, F). ARIZONA: Co.?: Gila River Valley, *Mohr in 1873* (F, type of *Euphorbia pseudoserpyllifolia* Millsp.). Mohave Co.: Yucca, *Jones in 1884* (P). Yuma Co.: Quartzsite, *Jones 24874* (P, CA). Maricopa Co.: Gila Bend, *Harrison & Kearney 7990* (F). Pinal Co.: Casa Grande, *Jones in 1884* (P). Greenlee Co.: San Francisco Mts. near Clifton, *Greene in 1880* (F). Cochise Co.: Bowie, *Jones 4223* (P, F marked "type" of *Euphorbia pseudoserpyllifolia* Millsp. by Millspaugh). NEW MEXICO: Co.?: no loc., *Wright 1854*, type collection of *E. micromera*, (G, F) Doña Ana Co.: 3 mi. W. La Mesa, Mesilla Valley, *Fosberg S4024* (P). MEXICO: Coahuila: Nassus River, Torreon, *Palmer 494 in 1898* (F, C). Lower California: Socorro, northern Lower Calif., *Orcutt 1331 in 1886* (F, G, C, D).

The inclusion of plants with stout stems and thickened nodes and pubescent herbage, and with slender stems and glabrous herbage in one entity is the only course which will not result in chaos, for all combinations of these vegetative characters occur. The reproductive and associated organs are very uniform and distinctive.

14. EUPHORBIA LATA Engelm. in Torr., Mex. Bound Survey, 188. 1859. *Chamaesyce lata* (Engelm.) Small, Fl. SE U. S., 1333, 1903. *Euphorbia dilata* Torr. & Gray, Pacific Rail. Rep. II 2: 175. 1861, not Hockst. or E. Mey. *Euphorbia rinconis* Jones, Con. West. Bot. 12: 76. 1908.

Perennial; stems ascending or erect, 10–15 cm. long, 0.5–1 mm. thick, with appressed short hairs, internodes 0.5–2 cm. long; leaves with short appressed hairs, blades ovate-deltoid-falcate to long deltoid or virtually linear in some cases by revolution of the margins, margin entire, more or less revolute, petioles ca. 1 mm. long; involucre solitary in the axils, turbinate, 1.75–2 mm. in diam., with short appressed hairs without, glabrous within except above; lobes deltoid, entire, equaling or exceeding the glands; glands transversely oblong, ca. 0.5 mm. long, hairy beneath; appendages absent or very narrow, white, crenate; fifth gland minute or absent, with a tuft of hairs in its interval; sinus somewhat depressed; bracteoles united below into one radial appendage adnate below to the involucre opposite each gland, 4–7 parted above, not quite equaling the glands, with straight long slender hairs above; andropeds 5–7 per fascicle, 25–35 per involucre, equaling the glands, with numerous hairs above; gynoped hairy, shortly exserted and reflexed at maturity; ovary with short appressed hairs, three-angled, styles ca. 0.75 mm. long, parted to or below the middle, with very short hairs below; capsule sharply three-lobed, with appressed hairs, ca. 2.5 mm. long, 2.5 mm. diam.,

axis persistent after dehiscence; seeds quadrangular, 2 mm. long, 1 mm. radially and tangentially, long-deltoid radially, back rounded, face straight in tangential silhouette, base obtuse-truncate, angles sharp, facets smooth, depressed, coat white, microreticulate.

Type locality: "Western Texas." Distribution: plains of Colorado and Kansas southward into Coahuila, Mexico. Representative specimens seen: COLORADO: Bent Co.: Las Animas, *Osterhout* 3923 (P). NEW MEXICO: *Fendler* 794 (F, G). Doña Ana Co.: Rincon, *Jones in 1890* (P, type of *Euphorbia rinconis* Jones); S of the White Sands, *Wootton in 1899* (C, D, P). Chaves Co.: 20 mi. S Roswell, *F. S. & E. S. Earle* 284 (P). TEXAS: Culberson Co.: Van Horn, *Jones* 26019 (P). Reeves Co.: Pecos, *Hanson* 780 (G), *Tracy* 104 (G). Crockett Co.: Ozona, *Jones* 26015 (W). Tom Green Co.: San Angelo, *Reverchon* 3795 (G), *Palmer* 10310 (D). Runnels Co.: Ballinger, *Neally in 1889* (F). Midland Co.: Midland, *Tracy* 7448 (F). Mitchell Co.: Colorado City, *Oyster in 1883* (F). Lubbock Co.: Lubbock, *Demaree* 7560 (G, D). Potter Co.: Amarillo, *Neally in 1888* (F). Hall Co.: Estelline, *Reverchon* 4303 (P). OKLAHOMA: Texas Co.: Camp, *Stevens* 406 (G), 403 (G). Beaver Co.: 15 mi. SW Beaver City, *Stevens* 349 (G, D). Harmon Co.: Hollis, *Stevens* 1067 (P, D, G). KANSAS: Grant Co.: Ulysses, *Thompson* 20 (G, C). Trego Co.: no loc., *Hitchcock* 474 (G). MEXICO: Coahuila: Peña, *Purpus* 1098 (C); Novano, *Purpus* 4511 (C); San Lorenzo de Laguna 22-27 leagues SW Parras, *Palmer* 1205 in 1880 (F).

The collections from Mexico are atypical in that the leaves are not falcate and the margins are plane but the hairs are present on the andropeds and the seeds are typical.

The collection: 15 mi. N Magdalena, Sonora Mex., Fosberg 7430 (UCLA); reported by Fosberg & Ewan, Bull. So. Cal. Acad. Sci. 34: 178-179. 1935, as the first record of *E. lata* from Sonora, is *E. pediculifera* var. *typica* and is cited under that species.

15. EUPHORBIA ACUTA Engelm., Bot. Mex. Bound., 189, 1859. *Chamaesyce acuta* (Engelm.) Millsp., Field Mus. Pub. Bot. 2: 407. 1916. *Euphorbia acuta* Engelm. var. *stenophylla* Boiss., DC. Prod. 15²: 18. 1862.

Perennial from a taproot as much as 1 cm. thick; stems annual, erect or ascending, numerous, 10-30 cm. long, to 1.5 mm. diam., with long weak hairs partially deciduous in age, internodes 1-4 cm. long; leaves sessile or subsessile, sparingly long villous below, less so and glabrate above, mostly 1-2 cm. long, ovate-lanceolate to lanceolate, base sub-symmetrical, apex long-acuminate, cartilaginous at the extreme tip, margin sometimes strongly revolute; stipules apparently wanting; peduncles stout, to 2 mm. long, sparingly to densely

villous; involucre solitary in the axils, turbinate, 1.75–2.5 mm. diam., sparsely to markedly villous without, with fine short hairs within; lobes narrowly deltoid and entire, or broader and two-toothed, equaling or slightly exceeding the glands; glands transversely elongate, slightly concave, ochroleucous, the proximal 1–1.5 mm. long, the distal shorter; appendages mostly wanting, when present to a little wider and longer than the glands, glabrous, white, margin with irregular short blunt teeth; fifth gland totally absent; sinus somewhat depressed, U-shaped; bracteoles 3–5 opposite each gland, united at the base and sometimes throughout, of various lengths, some usually nearly equaling the glands, long hairy; andropeds 4–5 per fascicle, 20–25 per involucre, 2.2–2.5 mm. long, slightly exserted, with from few to numerous slender hairs throughout; gynoped hairy, exserted and reflexed at maturity; ovary densely white hairy, styles glabrous, ca. 1 mm. long, parted to the middle, divisions somewhat flattened, recurved; capsule sharply three-lobed, 3 mm. long and diam., short appressed-hairy, axis persistent; seeds quadrangular, ovate radially, 2.2–2.5 mm. long, 1.5–1.7 mm. tangentially, 1.5 mm. radially, base oblique, coat white, microreticulate.

Type locality: "W Texas along the San Pedro & Pecos Rivers." Distribution: New Mexico, Texas and Coahuila. Specimens seen: NEW MEXICO: Co.: no locality, *Wright* #1840 (G, F fragment of type of var. *stenophylla* Boiss.), *Wright* 1739 (G). Eddy Co.: Hope *Jones* 26013 (P); Carlsbad, *Benke* 5034 (G, F). TEXAS: Rio Bravo del Norte, *Schott in* 1852 (F); River Pecos, San Pedro, (sic on copied label) *Wright* #1839 (F, apparently fragment of the type). Reeves Co.: Pecos City, *Neally in* 1889 (F). Pecos Co.: Fort Stockton, *Whitehouse* 8419 (F); Crockett Co.: Ozona, *Jones* 26015 (P). Valverde Co.: Del Rio, *Jones* 26014 (P). Uvalde Co.: Utopia, *Palmer* 10228 (D); West of Uvalde, *Jones* 28439 (C). MEXICO: Coahuila: 100 miles N Monclova, *Palmer in* 1880 (G); Diaz, *Pringle* 8278 (F, P, G, C).

16. *EUPHORBIA PENINSULARIS* Johnston, U. Calif. Pub. Bot. 7: 440. 1922.

Annual; stems to 25 cm. long, ascending or erect, few to several from the base, reddish brown, sparsely tomentose, internodes of the main branches often 3–4 cm. long, consequently the habit lax; petioles ca. 1 mm. long, leaf blades entire, sparsely short appressed-tomentose, often reddish brown in age, of two sorts: the first thinnish, oblong, 1–3 cm. long, with very slightly revolute margin and markedly oblique base, on the main branches; the second thickish, narrower to often linear by extreme revolution of the margin, these mostly on short lateral branches; stipules ca. 0.5 mm. long, consisting of 3–5 sparsely hairy linear segments on either side of the stem; peduncles up to 1 mm. long, sparsely short tomentose; involucre congested in glomerules on short leafy lateral branches, campanulate, 1.5 mm. diam., with short spreading

hair. without, glabrous within except just below the glands and on the lobes; lobes deltoid attenuate, slightly exceeding the glands; glands transversely oblong, concave; appendages conspicuous, white, glabrous, mostly ca. 1 mm. wide and 2 mm. long; fifth gland absent, its sinus U-shaped and slightly depressed; bracteoles numerous, forming a radial appendage opposite each gland, bracteoles of each appendage united below and adnate to the involucre for almost the whole length of the outer bracteoles, more or less hairy above; andropeds ca. 4 per fascicle, 20 per involucre, ca. 1.5 mm. long, glabrous, slightly exserted; gynoped glabrous except above; ovary densely straight-hairy, very slightly lobed; styles glabrous, 0.7–0.8 mm. long, parted to below the middle, slender; capsule sparsely hairy, ca. 2 mm. long and diam., widest at base and tapering upwards, carpels acutish on back but angles between the carpels only very slightly reëntrant; seeds sharply quadrangular, ca. 1.4 mm. long; ca. 1 mm. tangentially, ca. 0.8 mm. radially, ovate radially, base truncate, facets concave, with slight transverse wrinkles, white coat very thin, the brown testa showing through.

Type locality: San José del Cabo, Lower California. Distribution: south end of Lower California. Specimens seen: San Antonio [of the seven odd towns by this name in Lower California this is evidently the southernmost judging by the itinerary, *Con. West. Bot.* 17: 13. 1930.] *Jones* 22737 in 1926 (P); San José del Cabo, *Purpus* 325 (C, type), *Purpus* 7838 (G), *T. S. Brandegee* in 1890 (C); Cape San Lucas, *Craig* 629 (P).

17. *Euphorbia apicata* Wheeler n. sp.

Planta prostrata, perennis, cum capillis brevibus appressis crispisque praeter facies superiores foliorum; caulibus tenuibus, cum diametro minus 1 mm., internodis usque ad 3 cm. longis, ad summas brevioribus; stipulis dorsalibus ventralibusque ambis distinctis, linearibus, ca. 0.3 mm. longis; laminis foliorum integris, 3–7 mm. longis, ovato-oblongis, apice subacuto, base parum obliqua; petiolis ca. 0.5 mm. longis; pedunculis ca. 1 mm. longis; involucris in axillis solitariis sed in capitulis ad extremitates ramulorum plerumque congestis, involucris extra cum capillis paucis brevibus porrectis, intus glabris, cum diametro ca. 1 mm.; lobis glandulas leviter excedentibus, deltoideis, acutis, integris, cum capillis paucis brevibus porrectis in apice; glandulis nigropuniceis, transverso-oblongis, proximis ca. 0.5 mm. longis, distalis brevioribus; appendiculis conspicuis, glabris, albis, cum margine integra vel inaequaliter crenulata, usque ad 1.2 mm. longis et 0.5 mm. latis; glandula quinta ca. tertiom longitudinem sinus, late triangulare, cum capillis paucis porrectis; sinus late U-formato, leviter depresso; bracteolis quam andropedibus leviter brevioribus, 4–6 quaque glandula oppositis infra connatis et ad involucrem adnatis appendiculum radialem facientibus, parte libera bracteolarum cum capillis brevibus supra; andropedibus 4–5 in fasciculo singulo, 20–25 in involucre, glabris, leviter exsertis, ca. 1 mm. longis; gynopede

glabro (cum capillis paucis brevibus in apice), longo-exserto et in maturitate plerumque reflexo; ovario cum capillis leviter crispis brevibus; stylis prope ad basim partitis, tenuibus, leviter clavatis, glabris, ca. 0.3 mm. longis; capsula cum capillis paucis brevibus fere porrectis, distincte 3-angulata, dorsis carpellorum et linea conjunctionis carpellorum brunneis; seminibus debile albo-brunneis, radiale ovata-acutis, cum base truncata et depresso, ca. 0.8 mm. longis, tangentialia ca. 0.5 mm., radiale ca. 0.5 mm., seminibus quadrangularibus, angulis acris, lateribus planis, leviter rugulosis, apice cum mucrone brevissimo inflexo; axe capsulae persistente.

Type locality: Sierra de la Laguna, Lower California. Known only from the type: Sierra de la Laguna, [Lower] California, T. S. Brandegee, Oct. 2, 1899 (C sheet #110779). Although the heading of the label reads "California" the locality Sierra de la Laguna is well known in Lower California and no such locality name seems ever to have been used in California. That T. S. Brandegee was in Lower California about the date the type was collected is evidenced by Brandegee's collection of *Agave Brandegei* Trelease made in Cape region mountains, Lower California, Sept. 20, 1899, cited by Trelease, Ann. Rep. Mo. Bot. Gard. 22:57. 1911. In view of this evidence it seems reasonable to assume that Brandegee chanced to use the wrong label form for this *Euphorbia*.

In addition to the differentiae given in the key this species is distinguished from *E. peninsularis*, its nearest relative, by the shorter seeds and andropeds in *E. apicata*.

18. EUPHORBIA MELANADENIA Torrey, Pacif. Rail. Rep. 4: 135. 1857. *Anisophyllum melanadenium* (Torr.) Klotzsch & Garcke, Abh. Akad. Berl. 1859 (1860) 23. *Chamaesyce melanadenia* (Torr.) Millsp., Field Mus. Pub. Bot. 2: 410. 1916. *Euphorbia cinerascens* Engelm. var. *appendiculata* Engelm., in Torr., Bot. Mex. Bound., 186. 1859. *E. polycarpa* Benth. var. *appendiculata* (Engelm.) Munz, Bull. So. Cal. Acad. Sci. 31: 68. 1932. *E. polycarpa* Benth. var. *vestita* Wats., Bot. Cal. 2: 73. 1880. *Chamaesyce aureola* Millsp., Field Mus. Pub. Bot. 2: 406. 1916.

Perennial from a taproot as much as 5 mm. diam.; stems ascending or erect, to 20 cm. long, sometimes stout (1.5 mm. diam.) below, closely tomentose, glabrate; leaf blades 2-5 mm. long, ovate to ovate-lanceolate, base oblique, closely and often hoary tomentose on both surfaces, petioles clothed as the leaves, mostly ca. 1 mm. long; ventral stipules mostly united, linear, hairy, to 1 mm. long, dorsal stipules distinct, linear, hairy, to 1 mm. long; peduncles less than 1 mm. long, with short appressed hairs; involucre solitary in the axils, open-campanulate, 1.25-1.5 mm. diam., appressed short hairy without, glabrous within except below the glands; lobes narrowly deltoid, copiously hairy, equaling the glands; glands transversely oblong, dark red-

dish; appendages usually conspicuous, twice as wide as and longer than the glands to rarely wanting, white, margin crenate to subentire, glabrous or rarely with a few short hairs beneath next to the gland; fifth gland absent; sinus U-shaped, not depressed, densely hairy; bracteoles more or less completely united into an upwardly broadening, densely hairy, thickish, radial appendage adnate on the lower half to the involucre opposite each gland; andropeds 3-4 per fascicle, 15-20 per involucre, 1.5-2 mm. long, glabrous or rarely with short hairs above; gynoped shortly appressed-hairy, exerted and reflexed at maturity; ovary copiously hoary-tomentose, roundly three-lobed; styles parted nearly to the base, 0.5-0.8 mm. long, short-hairy below, slender throughout; capsule 1.5-1.75 mm. long, ovoid, sharply angled, very short tomentose; seeds quadrangular, 1.25-1.5 mm. long, ca. 0.6 mm. radially, ca. 0.6 mm. tangentially, facets smooth or slightly wrinkled, apex acutish, coat white, microreticulate.

Type locality: "San Gabriel," California. Actually probably the foot of the San Gabriel Mts. a few miles north as this is a foothill plant. Distribution: southern California, southwestern Arizona, northwestern Lower California and Guadalupe Island. Representative specimens seen: CALIFORNIA: Los Angeles Co.: Santa Monica Mts. (Sierra Santa Monica): no locality, *Hasse in 1890* (F); Cahuenga Pass, *Brewer 178* (C); Coldwater Canyon, *Peirson 4441* (Peir). Griffith Park, Los Angeles, *Epling in 1925* (UCLA); La Tuna Canyon, Verdugo Mts. (Range), *Ewan 4169* (P, C, CA, UCLA, Peir); Pasadena, *Kennedy in 1893* (P); San Gabriel, *Bigelow without date or number* (F, fragment of type of *Euphorbia melanadenia* Torr.), *Brewer 171* (C, wrong number fide note on sheet); Azusa, *Smith 4933* (F, type of *Chamaesyce aureola* Millsp.); 2 mi. NE La Verne, *Wheeler 9* (W, CA, UCLA); San Gabriel Mts.: Arroyo Seco at 1250 ft., *Peirson 310* (Peir); Santa Anita Canyon, *Wheeler 2535* (W, P); Little Santa Anita Canyon, *Abrams 2633* (P, D); Rogers Canyon, *Wheeler 399* (W, UCLA); San Gabriel River, *Blake 892* (F); Liveoak Canyon, *Johnston 1806* (P, C); San Antonio Canyon, *Abbott in 1906* (P). San José Hills W Pomona, *Munz & Harwood 3289* (P, D), *3288* (P); Puente Hills S Pomona, *Munz, Street, & Williams 2288* (P, D). San Diego Co.: Palm Canyon, Borrego Valley, *Munz & Hitchcock 11338* (P); Box Canyon, Colorado Desert, *Munz & Hitchcock 12068* (C, P); Montezuma Valley near Warner's Hot Springs, *Jaeger in 1925* (C, P); Jacumba, *Munz 8079* (P), *Abrams 3660* (D); San Felipe, *Thurber 628* (F), *T. S. Brandegee in 1895* (C); Vallecito Canyon, Laguna Mts., *Peirson 4865* (Peir); Mountain Springs, *Ferris & Bacigalupi 8244* (C), *Jones in 1924* (P). Imperial Co.: Mountain Springs Grade, *Munz 11950* (P, C). ARIZONA: Mohave Co.: Hackberry, *Jones in 1884* (P, D). Yavapai Co.: Congress Junction, *Jones in 1903* (P, D). Maricopa Co.: Mammoth, *Neally 271* (F). Pinal Co.: Oracle, *Jones in*

1903 (P), *Eggleston 15950* (F). Gila Co.: Roosevelt Dam, *Goodding 717* (G). Pima Co.: Rincon Mts., *Blumer 3278* (F); Sabino Canyon, Santa Catalina Mts., *Thorner 216* (P, D, C). LOWER CALIFORNIA: El Llano de Santana, *T. S. Brandegee in 1889 in part* (C); El Rancho Viejo, *T. S. Brandegee in 1889* (F, C); Cantillas Canyon, *Orcutt 35* (F); San Quentin Bay, *Orcutt 2196* (F); Guadalupe Island, *Palmer 783 in 1889* (F, C).

The plant from Mt. Springs, San Diego Co., California, *Ferris & Bacigalupi 8244* (C) is atypical in having hairy andropeds. Likewise the collection: Santa Anita Canyon, San Gabriel Mts., Los Angeles Co., California, *Wheeler 2535* (W, P) also has hairy andropeds. As this collection was of very robust plants there may be a relation between the vigor of the plant and the presence of hairs on the andropeds. The "Cuphea-like" involucre galls occur on one collection from Arizona: Pima Co.: Rincon Mts., *Peebles & Kearney 8769* (F, P).

19. *EUPHORBIA CINERASCENS* Engelm., in Torr., Bot. Mex. Bound., 186. 1859. *Chamaesyce cinerascens* (Engelm.) Small, Fl. SE U. S., 710. 1903. *Euphorbia melanadenia* Torr. var. *subinappendiculata* Engelm., ex. Boiss., DC. Prod. 15²: 32. 1862.

Perennial, forming mats up to 50 cm. in diam.; stems to 30 cm. long; prostrate or decumbent, mostly slender (1 mm. diam.), closely tomentose; leaf blades 2–5 mm. long, ovate with oblique base to oblong with slightly oblique base, usually glabrous above, closely tomentose beneath, petioles tomentose, mostly ca. 1 mm. long; stipules hairy, ca. 0.5 mm. long, ventral united, linear, dorsal distinct, linear; peduncles less than 1 mm. long, with short appressed hairs; involucre solitary in the axils, turbinate, 1.25–1.5 mm. diam., appressed short hairy without, glabrous within except below the glands; lobes narrowly deltoid, copiously hairy, equaling the glands; glands transversely oblong, dark reddish-purple; appendages narrow or usually wanting; fifth gland absent; sinus U-shaped, not depressed, densely hairy; bracteoles forming a radial appendage opposite each gland, often united only below, with 5 or 6 very slender short hairy free segments above; andropeds 3–4 per fascicle, 15–20 per involucre, 1.5–2 mm. long glabrous, gynoped shortly appressed-hairy, exserted and reflexed at maturity; ovary copiously hoary-tomentose, roundly three-lobed; styles parted nearly to the base, 0.5–0.8 mm. long, short-hairy below, clavate; capsule 1.5–1.75 mm. long, ovoid, sharply angled, very short tomentose; seeds quadrangular, 1.25–1.5 mm. long, ca. 0.6–0.9 mm. radially, ca. 0.6–1 mm. tangentially, facets smooth or faintly wrinkled, oblong or often deltoid-oblong radially (i.e. wider below), base obtuse or truncate, apex acutish, coat white, microreticulate.

Type locality: "On the Rio Grande," Texas. Distribution: southwestern Texas, south through Coahuila to Taumalipas and San Luis Potosi. Representative specimens seen: TEXAS: Co.?: no locality, *Wright 534 in*

1850 (F); along the Rio Grande, *Wright 559 in 1849*, type collection?, (F). Brewster Co.: Bouquillas, *Parks in 1929* (F); Chisos Mts., *Moore & Steyermark 3266* (C). Valverde Co.: Del Rio, *Palmer 12342* (C), *Jones 28463* (P, C), *25997* (P). Maverick Co.: Eagle Pass, *Jones 28464* (P). Dimmit Co.: Carrizo Spring, *Jones 28461* (P, C). Zapata Co.: San Ygnacio, *Tharp 3542* (P). MEXICO: Chihuahua: Chihuahua, *Pringle 800* (F, C); Santa Eulalia Mts., *Pringle 51* (F). Coahuila: Sierra Mojada, *Jones in 1892* (P); Saltillo, *Palmer 91 in 1898* (C, F), *295 in 1902* (F). Tamaulipas: Jaumave, *Rozynski 454* (F). San Luis Potosi: Minas de San Rafael, *Purpus 5469* (F, C, G).

The collection from San Luis Potosi has the leaves arranged in strikingly opposite and discrete pairs rather than congested or turned at various angles but I have observed this same peculiarity in one plant of *Euphorbia albomarginata* T. & G., La Verne, Calif., *Wheeler 2580* (W). In this latter case the atypical plant was sterile and the surrounding fertile plants were typical. This character seems to be of no consequence.

I had intended (Bull. So. Cal. Acad. Sci. 33: 106. 1934) to reduce this species to a variety of another species. Further consideration, however, has led me to keep it as a species.

The specimen of this species mentioned as *Euphorbia melanadenia* Torr. var. *subinappendiculata* Engelm. ex Boiss. by Boissier, DC. Prod. 15²: 32. 1862, collected by Gregg at "Monterey Californiae" must have come from Monterey, Nuevo Leon, Mexico, for *E. cinerascens* does not occur in California and Gregg is known to have collected near Monterey, Mexico, as evidenced by the collection of *Oenothera Greggii* Gray var. *Pringlei* Munz, Saltillo, Coahuila, *Gregg 33*, cited by Munz, Am. Jour. Bot. 16: 711. 1929.

In a list of manuscripts and herbarium names taken up by Boissier in De Candolle's Prodrumus, 15². 1896, appended to Engelmann's article, "On the Euphorbiaceae in Candolle's Prodrumus," by the editors Trelease & Gray on page 445 of "Botanical Works of the late Geo. Engelmann" appears "*E. melanadenia* var. *subappendiculata*." This spelling of the varietal name differs from the "*subinappendiculata*" published by Boissier.

20. EUPHORBIA VALLIS-MORTAE (Millsp.) J. T. Howell, Madroño 2: 19. 1931.
Chamaesyce vallis-mortae Millsp., Field Mus. Pub. Bot. 2: 403. 1916.

Perennial, usually forming a dense rounded plant up to 15 cm. high; herbage hoary-tomentose throughout; stems usually arising from 2-4 cm. below the surface of the ground, this portion brown and glabrous, aerial portion to 1 mm. diam., internodes mostly 1-2.5 cm. long; but much shortened toward the tip thereby congesting the leaves and involucre; leaf blades suborbicular to oblong-ovate, mostly 4-8 mm. long; lower stipules united,

filiform, ca. 1 mm. long, densely hairy, upper stipules distinct, filiform, ca. 0.7 mm. long, densely hairy; peduncles stout, to 1.5 mm. long, densely hairy; involucre solitary in the axils, campanulate, ca. 2 mm. diam., densely hairy without, with long erect hairs extending halfway down within opposite glands; lobes with long ascending hairs within, equaling or slightly exceeding the glands, deltoid, entire; glands yellowish or reddish, transversely oblong, to 1 mm. long, the distal slightly shorter; appendages white, as wide as and a little longer than the glands, entire or crenulate, with numerous short hairs beneath and on the margins and a few above; fifth gland absent; sinus U-shaped, with long erect hairs at the bottom; bracteoles mostly united into one group opposite each gland, of 6–10 bracteoles, more or less united below, adnate to the involucre, sometimes with shorter bracteoles outside the androped fascicle, all hairy above; andropeds 3–5 per fascicle, 17–22 per involucre, ca. 2 mm. long, slightly exserted, sometimes with a few short hairs above; gynoped densely hairy, long-exserted and reflexed at maturity; ovary three lobed, densely hairy; styles ca. 0.5 mm. long, parted to the middle, short-hairy below; capsule tomentose, three-angled, 2 mm. long and diam.; seeds quadrangular, ca. 1.5 mm. long, ca. 0.75 mm. tangentially and radially, ovate radially, raphe straight, back rounded in tangential silhouette, base obtusely truncate, coat white, microreticulate.

Type locality: between Mohave and Keeler northwestern Mohave Desert, Calif., not Death Valley as stated by Millspaugh. Distribution: northwest Mohave Desert north to Owens Lake, California. Specimens seen: Co.?: Between Mohave & Keeler, *Coville & Funston 1008* (F, fragment of type). Inyo Co.: west shore Owens Lake, *Hall & Chandler 7323* (P, C). Kern Co.: Indian Wells, *Hoffmann 617* (P); 6 mi. N Freeman, *Hoffmann 585* (CA, SB); Red Rock Canyon, *Peirson 7335* (P, Peir), *Howell 4973* (Peir, CA); Dove Springs, *Hoffmann in 1931* (SB).

21. *EUPHORBIA PEDICULIFERA* Engelm. in Torr., Bot. Mex. Bound. Surv., 186. 1859. *Chamaesyce pediculifera* (Engelm.) Rose & Standley, Contr. U. S. Nat. Herb. 16: 12. 1912.

Perennial from a taproot stout in age; stems prostrate to erect, appressed pubescent, glabrate in age, up to 2 mm. in diam. toward the base, internodes up to 5 cm. long, often very short toward the stem tips thus congesting the involucre; leaves closely appressed pubescent to subglabrous, blades 2–30 mm. long, 1–10 mm. wide, ovate with oblique base, oblong with subsymmetrical base to spatulate and even narrowly linear with symmetrical base, petioles 1–2 mm. long, amplexicaul on ventral side of stem; stipules mostly less than 0.5 mm. long, the ventral united, the upper distinct; peduncles clothed as the leaves, up to 1.5 mm. long; involucre campanulate, 1.5–2 mm. long, solitary in the axils, sometimes congested at the branch tips by shortening of the terminal internodes but not strictly glomerulate, closely appressed

pubescent to sub-glabrous without, more or less short hairy within above; lobes deltoid, hairy, equaling the glands; glands transversely oblong, 0.5 mm. wide, 0.75–1.25 mm. long, dark red-purple; appendages absent or up to 2 mm. wide and 3 mm. long, entire or slightly lobed, glabrous; fifth gland very short or usually absent; sinus U-shaped, hairy, little depressed; bracteoles shorter than the andropeds, usually very hairy above, in one group of 6–8 opposite each gland, united at the base and adnate to the involucre; andropeds ca. 1.25 mm. long, included or shortly exserted, glabrous or with few hairs above, 4–5 per fascicle, 22–25 per involucre; gynoped nearly glabrous or hairy nearly throughout, exserted and reflexed at maturity; ovary very slightly lobed, densely hairy, tapering upward, styles ca. 1 mm. long, slender, parted to the base, short hairy on the lower side to the tip; capsule appressed pubescent, widest below the middle, 2 mm. in diam. and long, markedly three-lobed, the lobes obtuse, axis persistent; seeds cylindrical, 1–1.3 mm. long, 0.6–0.7 mm. diam. encircled by 4 or 5 rounded ridges with V-shaped channels between, coat white.

KEY TO VARIETIES

- Leaves ovate to lanceolate with obtuse apex; bracteoles 6–8, united only at base and conspicuous. 21a. var. *typica*
 Leaves strictly linear; bracteoles reduced, usually inconspicuous, if conspicuous, united upward. 21b. var. *linearifolia*

21a. *Euphorbia pediculifera* Engelm. var. *typica* Wheeler nom. n. *Euphorbia involuta* Millsp., Proc. Calif. Acad. Sci. II 2: 227. 1889. *Chamaesyce involuta* Millsp., Field Mus. Pub. Bot. 2: 410. 1916. *Euphorbia pediculifera* Engelm. var. *involuta* (Millsp.) Johnston, Proc. Calif. Acad. Sci. IV 12: 1070. 1924. *Euphorbia conjuncta* Millsp., Proc. Calif. Acad. Sci. II 2: 227. 1889. *Chamaesyce conjuncta* Millsp. Field Mus. Pub. Bot. 2: 408. 1916. *Euphorbia pediculifera* Engelm. var. *inornata* T. S. Brandegee, Zoe 5: 209. 1905. *E. vermiformis* Jones, Con. West. Bot. 16: 23. 1930.

Type locality: Sonora, Mexico. Distribution: southeastern California, Arizona, Lower California, Sonora, Sinaloa. Representative specimens seen: CALIFORNIA: Imperial Co.: Carrizo (Cariso) Mt., *T. S. Brandegee in 1905* (C); Midway Well, *Peirson 9796* (Peir, W); 20 mi. NE Ogilby, *Munz & Hitchcock 12155* (P). ARIZONA: Coconino Co.: Williams Fork, *Palmer 515 in 1876* (G). Yavapai Co.: Congress (C. Junction), *Jones in 1903* (D, P), *Orcutt in 1896* (C). Yuma Co.: Ehrenberg, *Palmer in 1876* (G). Maricopa Co.: Maricopa Mts. (Hills), *Pringle in 1882* (G); Gila Bend, *Harrison & Kearney 7896* (P, F). Pinal Co.: Mammoth, *Harrison & Kearney 6692* (P). Pima Co.: Hartts Ranch, *Thornber 122* (P, C); Gunsight Peak, *Fosberg 7434* (UCLA); Ajo, *Jones 24858* (C, P, G, CA in part), *Jones 24856* (P, type of *E. vermiformis*). Santa Cruz Co.: Nogales, *Peebles, Harrison & Kearney 4599* (UCLA, P), *5576* (UCLA), *8151* (CA). Cochise

Co.: Chiricahua Mts., Bowie (Fort B.), *Lemmon* 283 (C, G). LOWER CALIFORNIA: West Coast, *Com. Evers* of "Narragansett" in 1873 (G); Big Canyon, Tantillas Mts. 34 mi. from Tecate, *Palmer* 453 in 1875 (F, G); Santa Rosalia, *Jones* 22619 (P); Purisima, *T. S. Brandegee* in 1889 (G, C, isotypes of *Euphorbia conjuncta* Millsp.); Comondu, *T. S. Brandegee* in 1889 (C, isotype of *Euphorbia involuta* Millsp.); Los Angeles Bay, *Palmer* 631 in 1887 (G); Espiritu Santo Island, *Johnston* 3991a (C, CA, G), *Craig* 656 (P); La Paz, *Palmer* A in 1890 (C, G), *Jones* 24501 (P, UCLA). SONORA: No locality, *Schott*, no date or no. (G); Poso Verde, *Schott* III 12 in 1855 (F); 15 mi. N Magdalena, *Fosberg* 7430 (P, UCLA); Pitiquito, *Pringle* in 1884 (G, F); Hermosillo, *Jones* 22615 (G, P). SINALOA: Confradia, *T. S. Brandegee* in 1904 (F, G, C type of *Euphorbia pediculifera* Engelm. var. *inornata* T. S. Brandegee); Topolobampo, *Palmer* 212 in 1897 (G), *Rose*, *Standley & Russell* 13276 (F); San Blas, *Jones* 23324 (P).

Included in this variety is a great diversity of habit and leaf shape. It appears to me that the leaf shape varies more according to the situation in which the plant is growing than according to any innate tendency.

21b. EUPHORBIA PEDICULIFERA Engelm. var. LINEARIFOLIA Wats., Proc. Am. Acad. 24: 76. 1889.

Type locality: High Mts., Guaymas, Sonora, Mexico. Distribution: Guaymas and San Pedro Bay, Sonora. Specimens seen: SONORA: Guaymas, *Palmer* 627 in 1887 (F, G, C), *Palmer* 215 in 1887 (C, G type), *T. S. Brandegee* in 1893 (C); San Pedro Bay, *Craig* 671 (P).

22. EUPHORBIA FENDLERI Torr. & Gray, Pacif. Rail Rep. II 2: 175. 1855. *Anisophyllum Fendleri* (T. & G.) Klotzsch & Garcke, Abh. Akad. Berl., 1859 (1860) 26. *Chamaesyce Fendleri* (T. & G.) Small, Fl. SE U. S., 710. 1903. *Euphorbia rupicola* Scheele, Linnaea 22: 153. 1849, not Boissier.

Glabrous perennial from a taproot woody in age; stems several to numerous from the base, decumbent to erect, up to 15 cm. long, slender, internodes up to 2 cm. long; leaf blades entire, ovate-orbicular with oblique base to lanceolate, petioles mostly ca. 1 mm. long; stipules up to 1 mm. long, distinct, narrowly linear, mostly entire, rarely with a few hairs; peduncles up to 4 mm. long, glabrous; involucre solitary in the axils, glabrous, 1.25–1.75 mm. diam., campanulate to turbinate, glabrous without, with short hairs within above opposite the glands, lobes deltoid-shortly-attenuate, hairy within below, equaling the glands; glands reddish, 1.5–4 times as long as wide, concave or convex, up to 1 mm. wide; appendages white, glabrous, 0.5–1 mm. long, as wide as the gland at least at the base, obtuse-crenate to entire and narrowly deltoid, or parted into 2–4 narrow ligules; fifth gland shorter than the lobes, linear; sinus very broad and little depressed; bracteoles forming a single appendage adnate below to the involucre opposite each gland, 3–5 parted and

hairy above; andropeds 1.25 mm. long, glabrous, 5-7 per fascicle, 25-35 per involucre; gynoped glabrous, exerted and reflexed at maturity; ovary glabrous, three-lobed; styles glabrous, ca. 0.4 mm. long, bifid to the middle, curved upward, thickened at the base; capsule glabrous, spheroid, three-angled, ca. 2.25-2.5 mm. long, axis persistent; seeds quadrangular, 2-2.25 mm. long, ca. 1 mm. radially, 1-1.2 mm. tangentially, ovate-acute radially, angles prominent, front facets concave, mostly smooth, back facets slightly wrinkled, coat white, microreticulate.

KEY TO VARIETIES

Plants decumbent to erect; leaves ovate-orbicular to ovate-lanceolate; appendages obtuse, crenate..... 22a. var. *typica*
Plants erect and leaves lanceolate.

Appendages narrowly deltoid, entire..... 22b. var. *chaetocalyx*

Appendages parted into 3-4 narrowly linear segments; root very thick.....
..... 22c. var. *triligulata*

22a. *Euphorbia Fendleri* T. & G. var. *typica* Wheeler n. nom. *E. rupicola* Scheele. Linnaea 22: 153. 1849, not Boissier. *E. Fendleri* T. & G. var. *dissimilis* Payson, Bot. Gaz. 6: 379. 1915. *Chamaesyce Gooddingii* Millsp., Field Mus. Pub. Bot. 2: 406. 1916.

Type locality: "Big Springs of the Colorado, New Mexico." Probably somewhere near Sante Fe, New Mexico, fide Standley Contr. U.S. Nat. Herb. 13: 199. 1910. Distribution: California north to Utah, east to Kansas, and south to Sonora, Mex. Representative specimens seen: CALIFORNIA: Co.? : Desert Wells, Southeastern Calif., *Purpus 5689 in part* (C). San Bernardino Co.: Clark Mt. E Mohave Desert, *Jaeger in 1930* (P). Inyo Co.: Westgard Pass, White Mts., *Duran 547*, (P, C, D, CA, RS). NEVADA: Clark Co.: Charleston Mts.: Lee Canyon, *Heller 11058* (G, C, F type of *Chamaesyce Gooddingii* Millsp.); Kyle Canyon, *Jaeger in 1926* (P, CA). Lincoln Co.: Caliente, *Jones in 1904* (P). Esmeralda Co.: Candelaria, *Shockley 312* (C, D in part). UTAH: Duchesne Co.: Myton, *Jones in 1908* (P). Carbon Co.: Price, *Stokes in 1898* (C), *in 1900* (D), *Flowers 6390* (F). Grand Co.: Thompson's Springs, *Jones in 1891* (P). Beaver Co.: Frisco, *Jones in 1880* (P); Milford, *Jones in 1880* (P). Garfield Co.: Tropic, *Jones in 1894* (P). ARIZONA: Mohave Co.: Peach Springs, *Wilson in 1893* (C). Coconino Co.: Flagstaff, *Jones 336* (P). Yavapai Co.: Skull Valley, *Jones in 1903* (P). WYOMING: Laramie Co.: Hartville, *Nelson 8326* (P). COLORADO: Yuma Co.: Wray, *Eggleston 15201* (F). Montrose Co.: Naturita, *Payson 119*, fragment of type of *Euphorbia Fendleri* var. *dissimilis* (W); Paradox, *Walker 110* (P, D). Gunnison Co.: Barnum, *Eastwood in 1910* (C, CA). Fremont Co.: Canyon City, *T. S. Brandegees 866* (C), *Johnston & Hedgecock 739* (C). NEW MEXICO: Santa Fe Co.: Canoncito,

Heller 3727 (D); Big Springs of the Colorado, *Fendler 800*, type collection of *E. Fendleri* var. *typica*, (F). San Juan Co.: Farmington, *Osterhout 6948* (P); Aztec, *Baker 613* (P). Chaves Co.: 20 mi. S Roswell, *F. S. & E. S. Earle 313* (P). KANSAS: Trego Co.: no loc., date, or no., *Bodin* (F). Morton Co.: Richfield, *Thompson 167* (G). OKLAHOMA: Ellis Co.: Shattuck, *Stevens 2944* (D). Beaver Co.: Knowles, *Stevens 338½* (P). TEXAS: Kendall Co.: Baerne, *Palmer 9912* (D). Reeves Co.: Pecos, *Gillespie 5262* (D). Brewster Co.: Chisos Mts., *Ferris & Duncan 2920* (D). Randall Co.: Canyon, *Benke 4987* (F). Erath Co.: Dublin, *Maxwell 52* (F). Hood Co.: Granbury, *Reverchon in 1877* (F). Kerr Co.: Kerrville, *Heller 1870* (C). Travis Co.: Austin, *Hall 545 in 1872* (F, P). Comal Co.: "Comanche Springs, New Braunfels, etc.," *Lindheimer 1138*, type collection of *E. rupicola* Scheele, (C), *1137* (C). Bexar Co.: Leon Springs, *Clemens 425* (P).

The extreme forms of variety *typica* and *chaetocalyx* are readily distinguishable by the habit, leaf shape and appendages, but a complete series of intergrades exists. The following specimens are intergrades between var. *typica* and *chaetocalyx*: ARIZONA: Co.?: Between Jacob's Station and Houserock, Kaibab, *Jaeger in 1927* (P). NEW MEXICO: Co.?: San Ysidro, *Arsène 19052* (P), *19053* (F), *Arsène & Benedict 17541* (F). Bernalillo Co.: Albuquerque, *Jones in 1880* (P). Sierra Co.: Kingston, *Metcalfe 1488* (P, CA, F). TEXAS: Co.?: Indian Hot Springs, *Jones 25996* (P).

22b. *EUPHORBIA FENDLERI* T. & G. var. *CHAETOCALYX* Boissier DC. Prod. 15²: 39. 1862. *Chamaesyce chaetocalyx* (Boiss.) Wooton & Standley, Contr. U. S. Nat. Herb. 16: 144. 1913.

Type locality: New Mexico. Distribution: Arizona, New Mexico, and Western Texas. Representative specimens seen: ARIZONA: Mohave Co.: Peach Springs, *Greene in 1889* (F), *Wilson in 1893* (C). Coconino Co.: Cameron, *Hanson A212* (F). Navajo Co.: no loc., *Toumey in 1896* (F). NEW MEXICO: Co.?: no loc., *Wright 1847* (F, fragment of type from herb. Boissier). Socorro Co.: Socorro, *Eggleston 16238* (F). Doña Ana Co.: Conkling Cave, Pyramid Peak Range, *Fosberg S3245* (P). Otero Co.: High rolls, Lincoln Forest, *Eggleston 14407* (G). TEXAS: El Paso Co.: El Paso, *Jones 4217* (P). Culberson Co.: McKittrick Canyon, Guadalupe Mts., *Moore & Steyermark 3532* (C, CA). Brewster Co.: Chisos Mts. *Muel-ler 8074* (F).

22c. *Euphorbia Fendleri* T. & G. var. *triligulata* Wheeler n. var.

Radix multum crassa; caulibus erectis; foliis lanceolatis; appendiculis in 3-4 anguste linearibus segmentis partitis.

Type locality: Boquillas Canyon above Boquillas, Brewster Co., Texas. Known only from the type locality. Specimens seen: TEXAS: Boquillas Canyon above Boquillas, Brewster Co.; *Moore & Steyermark 3444 in 1931* (G, type; CA, D, isotypes).

23. EUPHORBIA ALBOMARGINATA Torr. & Gray, Pacif. Rail. Rep. 2: 174. 1855. *Chamaesyce albomarginata* (T. & G.) Small, Fl. SE U. S., 710. 1903. *Euphorbia stipulacea* Engelm. ex Boissier, (in synonymy), DC. Prod. 15²: 30. 1862.

Glabrous prostrate perennial from a taproot woody in age; stems several to numerous, up to 30 cm. long, internodes up to 6 cm. long but usually much shorter, nodes often rooting; leaf blades mostly 3–6 mm. long, sometimes as much as 15 mm. long, orbicular to oblong, sometimes with a red spot in the middle on the upper surface, midrib usually not prominent, lateral veins rarely evident, margin entire, petioles 0.5–1 mm. long; both upper and lower stipules united into a glabrous, white, membranous, deltoid to subulate, usually lacerate-margined scale; peduncles slender, glabrous, mostly 2–4 mm. long; involucre solitary in the axils, 1.5–2 mm. diam., open-campanulate to turbinate, glabrous without and within; lobes short-hairy within below, exceeding the glands, narrowly deltoid-attenuate; glands 0.5–1 mm. long, transversely oblong, concave, ochroleucous or mostly maroon; appendages usually conspicuous, wider and longer than the glands, white, glabrous, entire or slightly crenate; fifth gland linear, equaling the lobes, hairy within below; sinus U-shaped, little depressed; bracteoles forming one conspicuous, upwardly expanded, mostly 2–4 divided, hairy radial appendage two-thirds as long, to as long as, the andropeds, adnate below to the involucre opposite each gland; andropeds 1–1.3 mm. long, glabrous, 3–6 per fascicle, 15–30 per involucre; gynopod glabrous, long-exserted and mostly reflexed at maturity; ovary glabrous, three-lobed, styles bifid to below the middle, ca. 0.5 mm. long, glabrous, clavate, spreading-erect; capsule sharply three-angled, glabrous, ovoid, ca. 1.75 mm. long; seeds 1.3–1.4 mm. long, ca. 0.6 mm. radially and tangentially, quadrangular, narrowly oblong radially, base obtuse or truncate, facets concave or convex, smooth, angles mostly rounded, coat microreticulate in definite lines, opaque-white or so thin as to little obscure the brown testa; capsule axis persistent.

Type locality: Not stated. Distribution: California, northeast to Utah, southeast to Texas and Sonora. Representative specimens seen: CALIFORNIA: Inyo Co.: Surprise Canyon, Panamint Mts., *Ferris 7951* (P, D), *Howell 4040* (CA); Shepherd's Canyon, Argus Mts., *Coville & Funston 735* (D); Emigrant Springs, *Parish 10086* (F, C). Kern Co.: Canyon W Cuddy Canyon, Mt. Piños Region, *Munz 7061a* (P); Ft. Tejon, *Abrams & McGregor 284* (D). Los Angeles Co.: Lancaster, *Elmer 3630* (CA, P, C); Inglewood, *Abrams 2480* (P, C, D). San Bernardino Co.: Mohave Desert:

7 mi. S Barstow, *Johnston 6498* (P); Cactus Flat, San Bernardino Mts., *Munz 10511* (P); Redlands, *Budd in 1901* (P, D). Riverside Co.: Corona, *Munz & Harwood 3247* (P); Whitewater, *Vasey 443* (F). San Diego Co.: San Felipe, *Jones in 1906* (P). Imperial Co.: Durmid, *Parish 8066* (D). NEVADA: Clark Co.: Colorado River bottoms 15 mi. E Searchlight, *Parish 10290* (F, C). Lincoln Co.: Caliente, *Jones in 1904* (P). UTAH: Washington Co.: St. George, *Jones 1663* (P, CA). ARIZONA: Mohave Co.: Hackberry, *Jones in 1903* (P). Coconino Co.: Grand Canyon of the Colorado, *Mills-paugh 149* (F). Yavapai Co.: Humboldt, *Peebles & Harrison 4117* (UCLA). Maricopa Co.: Aguila, *Jones 26002* (P); Phoenix, *Jones in 1903* (P). Pinal Co.: Superior, *Peebles, Harrison & Kearney 5076* (UCLA). Pima Co.: Babiroquivra Mts., *Jones 24852* (UCLA, C, CA, P). NEW MEXICO: Grant Co.: Cliff, *Eggleston 19990* (F). Sierra Co.: Kingston, *Metcalfe 1101* (P, CA, F). Luna Co.: Deming, *Jones 3802* (P, CA). Doña Ana Co.: south end Organ Mts., *Fosberg S3212* (P). Lincoln Co.: Gray, *Skehan 8* (P, F, C). Chaves Co.: 20 mi. S Roswell, *S. F. & E. F. Earle 309* (P). TEXAS: Presidio Co.: Presidio, *Harvard, no date or no.* (F). Brewster Co.: banks of Rio Grande, Boquillas Canyon, *Moore & Steyermark 3432* (CA). Bexar Co.: San Antonio, *Sculy 2160* (P). Webb Co.: Laredo, *Palmer 11274* (C). OKLAHOMA: Harmon Co.: Hollis, *Stevens 1105* (G, D). BAJA CALIFORNIA: 50 mi. SE Tecate, *Munz 9553* (P). SONORA: 15 mi. N Magdalena, *Fosberg 7429* (UCLA, D, P); Hermosillo, *Rose, Standley & Russell 12446* (F). Guaymas, *Palmer 93 in 1887* (C). CHIHUAHUA: Casas Grandes, *Goldman 406* (F, G); Chihuahua, *Palmer 371 in 1908* (F). SINALOA: Culiacan, *T. S. Brandegee in 1904* (F, C), *Rose, Standley & Russell 14931* (F, G), *Goldman 372* (F, G). COAHUILA: Sabinas, *Nelson 6792* (F). DURANGO: Durango, *Palmer 296 in 1896* (F, C); Santiago Papasquiaro, *Palmer 42 in 1896* (F, C).

In the California plants the white seed coat is very thick. In most of the plants from elsewhere this coat is very thin so that the seeds appear brownish. Some plants in Arizona, as Babiroquivra Mts. *Jones 24852* have large, obtuse, and veiny leaves. The following local peculiarities are noted from California: San Bernardino Co.: Fimbriate beneath the capsule, Cactus Flat; stipules adnate to petioles, 7 mi. S Barstow. Inyo Co.: Surprise Canyon, Panamint Mts., *Ferris*, stipules distinct but membranous.

Occasionally the leaves have a red maculation in the center. There is an apparently unpublished herbarium name based on this character.

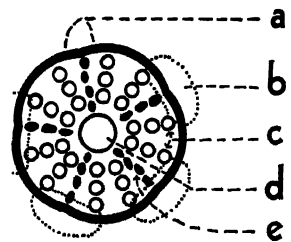
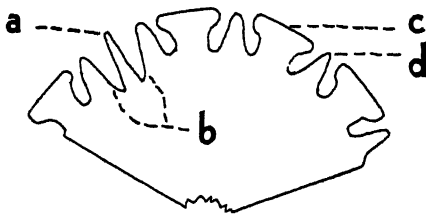
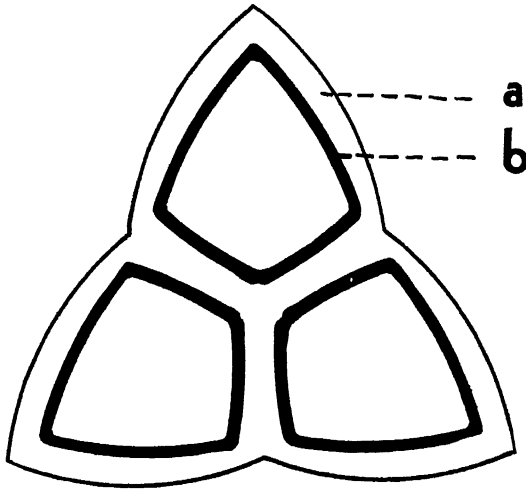
24. EUPHORBIA SERPENS H. B. K., Nov. Gen. et Sp. 2: 52. 1817, not Baill., or Balb. ex Boiss. *Anisophyllum serpens* (H. B. K.) Klotzsch & Garcke,

Phys. Abh. Akad. Wiss. Berlin, 1859 (1860) 23. *Chamaesyce serpens* (H.B.K.) Small, Fl. SE U. S., 709. 1903. *Euphorbia serpens* H.B.K. *A. genuina* Thellung, in Aschers. & Graebn., Syn. Flora Mittel. 7: 442. 1916. *E. serpens* H.B.K. var. *imbricata* Boiss., DC. Prod. 15²: 30. 1862. *E. serpens* H.B.K. *A. genuina* Thellung II *imbricata* (Boiss.) Aschers & Graebn., Syn. Flora Mittel. 7: 442. 1916. *E. serpens* H.B.K. var. *radicans* Engelm. ex Boiss., DC. Prod. 15²: 30. 1862. *E. radicans* Moric [in Berland pl. exs.], nach Klotzsch & Garcke, Phys. Abh. Akad. Wiss. Berlin, 1859. 24 (1860), (as a synonym of *Anisophyllum serpens*). *E. Engelmannii* Sennen var. *radicans* (Moric) Sennen & Pau, in Sennen pl. d.'Esp. n. 1442, Bull. Geogr. bot. 23^e annee [Ser. 4^e] Nr. 295/7. 230. 1914. *Chamaesyce radicans* (Moric) Millsp., Field Mus. Pub. Bot. 2: 411. 1916. *Euphorbia herniaroides* Nutt., Pl. Arkans., 171. 1837. *E. flexicaulis* Scheele, Linnaea 22: 154. 1849. *E. serpens* H.B.K. *A. genuina* Thellung III *flexicaulis* (Scheele) Thellung in Aschers. & Graebn. Syn. Fl. Mittel. 7: 442. 1916.

Prostrate annual, often very leafy, herbage glabrous throughout; stems slender, up to 30 cm. long, internodes to 3 cm. long, nodes sometimes rooting; leaf blades 2–7 mm. long, ovate-orbicular to oblong, base oblique except in the smallest, margin entire, petioles mostly less than 1 mm. long; both upper and lower stipules united into a white, membranous, glabrous scale less than 1 mm. long with more or less lacerate margin; peduncles up to 2 mm. long, expanding upward, glabrous; involucre solitary in the axils, turbinate, 1 mm. long, 1 mm. diam., tapering to the thick upper end of the peduncle, glabrous without and within; lobes deltoid, sometimes with a few hairs on the margins below, apex acute to attenuate, equaling or slightly exceeding the glands; glands transversely oblong, ca. 0.2 mm. long, ochroleucous, concave; appendages mostly present, little wider than the glands, white, glabrous, margin mostly crenate; fifth gland linear, exceeding the glands, with a few marginal hairs at the base; sinus slightly depressed; bracteoles forming a single, linear or broader, entire or parted, slightly hairy appendage 0.6 mm. long or shorter, adnate below to the involucre opposite each gland; andropeds 5 per involucre, glabrous, 1 mm. long, equaling the glands; gynoped glabrous, exserted and mostly reflexed at maturity; ovary 3-lobed, glabrous, styles glabrous, markedly clavate, 0.2 mm. long, usually parted to below the middle, rotately spreading; capsule glabrous, 3-angled, ca. 1.2 mm. long; seeds ovoid with rounded angles or somewhat turgid-quadrangular with more prominent angles, ca. 1 mm. long, ca. 0.5 mm. radially and tangentially, coat microreticulate, white, with the brown testa showing through; capsule axis persistent.

Type locality: Cumana, Venezuela. Distribution: Illinois, Iowa, Kansas, and Colorado southward through Mexico to South America. Representative specimens seen: NEW MEXICO: Doña Ana Co.: Mesquite, *Fosberg S3615* (P, C). Eddy Co.: Carlsbad, *Tracy 8170* (F). Weld Co.: New Windsor, *Osterhout in 1899* (P, F). Fremont Co.: Canyon City, *T. S.*

Brandegee in 1873 (C). NORTH DAKOTA: Barnes Co.: Kathryn, *Bexgmen* 971 (F). KANSAS: McPherson Co.: Lindsborg, *Bodin in 1884* (F). Hamilton Co.: Syracuse, *Thompson 136* (C). OKLAHOMA: Ottawa Co.: Miami, *Stevens 2305* (P). TEXAS: Dallas Co.: Dallas, *Reverchon in 1879* (F). Travis Co.: Austin, *Hall in 1872* (P, F). Hayes Co.: San Marcos, *Palmer*



Explanatory diagrams of the reproductive structures of *Euphorbia*, sect. *Anisophyllum*

Fig. 1. Diagrammatic transverse section of capsule. a. Carpel wall. b. Seed testa.

Fig. 2. Diagram of involucre spread open. a. 5th gland. b. Sinus. c. Gland. d. Involucral lobe.

Fig. 3. Diagrammatic transverse section of involucre cut just below the intervals between the glands and the lobes. a. Interval of reduced 5th gland. b. Silhouette of gland to show its relative position. c. Andropeds. d. Gynopeds. e. Bracteole.

12095 (C). Comal Co.: New Braunfels, *Lindheimer* 693, type collection of *Euphorbia serpens* var. *imbricata* Boiss., (F). Bexar Co.: San Antonio, *Bebb* 2364 (F), *Clemens* 421 (P), *Jermy* 130 (G). Gonzales Co.: No loc., *Bogusch* 936 (F). Nueces Co.: Corpus Christi Bay, *Heller* 1467 (P, C, UCLA). Brazoria Co.: Columbia, *Palmer* 6679 (F). Starr Co.: Rio Grande City, *Neally in* 1889 (F). MISSOURI: Jefferson Co.: St. Louis, *Glatfelter in* 1894 (F). ARKANSAS: Pulaski Co.: Little Rock, *Hasse in* 1886. TENNESSEE: Davidson Co.: Nashville, *Gattinger (Curtiss)* 2500 (F). LOUISIANA: Plaquemines Co.: Port Eads, *Tracy & Lloyd* 210 (F). FLORIDA: Escambia Co.: Pensacola, *Curtiss* 5920 (C, D). LOWER CALIFORNIA: Comondu, *T. S. Brandegee in* 1889 (F). SONORA: Lerdo, *Palmer* 954 *in* 1889 (F). COAHUILA: San Lorenzo Laguna, 22-27 leagues SW Parras, *Palmer* 1192 *in* 1880 (F). TAMAULIPAS: Tampico, *Palmer* 521 *in* 1910 (F, CA). SAN LUIS POTOSI: San Dieguito, *Palmer* 121 *in* 1910 (F, C). GUATEMALA: Department of Retahulen: Mulua, *Kellerman* 5173 (F).

The plant from Lower California, although far out of range, is typical. There may have been an error in labeling.

I have not seen type material of this species and consequently the entity here called *Euphorbia serpens* H.B.K. may not be identical with the Venezuelan plant.

EXCLUDED OR DOUBTFUL SPECIES

1. *EUPHORBIA CAPITELLATA* Engelm. ex. Torrey, Bot. Mex. Bound. Surv. II 2: 188. 1859. See Bull. Torrey Club 62: 537. 1935 for synonymy.

This species is sometimes entire-leaved and might be thought to belong in this group but usually at least a few of the leaves are serrate.

2. *CHAMAESYCE TAMAULIPASANA* Millsp., Field Mus. Pub. Bot. 2: 403. 1916.

Although described as entire-leaved by Millspaugh the type has many of the leaves definitely serrate which character excludes it from this group if geographical considerations do not. Although this species is valid as far as I know I refrain from making a new combination of it until I study related species.

GRAY HERBARIUM,
HARVARD UNIVERSITY,
CAMBRIDGE, MASS.

The structure of the growing point and the development of the bud scales of *Morus alba*¹

G. L. CROSS

(WITH SIXTEEN TEXT-FIGURES)

In most text books of botany bud scales are described as transformed or modified foliage leaves. The general applicability of this interpretation seems uncertain on the grounds of insufficient knowledge. Recent researches indicate that very little is known about the developmental mechanics of foliar structures other than foliage leaves. As far as the writer has been able to discover, Foster (1935) has provided the only complete histogenetic study of a bud scale to be found in the literature. Since the time of Grew numerous observations of the gross structure of scales have been made, and histological studies of mature tissues have occasionally appeared. A confusing array of interpretations based on such researches is presented to one who would review the literature, although Foster (1928) has provided a very helpful résumé to which students of foliar structures are referred.

Botanists differ concerning the value of ontogeny as a criterion of relationship, and admittedly, such evidence should be used with caution in making phylogenetic interpretations. When attempting to find the morphological category to which the organs of a given plant belong, however, it is necessary to determine all basic points of similarity and difference. Such definite information can be accumulated by studying the organs completely, i.e. throughout their ontogenetic processes, and will naturally involve a consideration of the origin and development of their primordia. Any morphological conclusions based on less complete information are apt to be inaccurate and misleading.

Although the morphological interpretation of bud scales has always been somewhat in doubt, the "transformation theory" supported by Goebel (1928) gradually became prominent during the first quarter of the twentieth century. Goebel developed the view that all foliar primordia are potential foliage leaves. When a bud scale is produced an "arrest" occurs in the development of a foliage leaf primordium after which this structure, by divergent development, becomes a scale. He based his conclusions upon morphological and experimental data which have been discussed by Foster (1928).

Recently the views of Goebel have been challenged by Foster, who has reattacked the problem from an ontogenetic viewpoint, and in a series of papers has presented evidence that foliage leaf and bud scale primordia

¹ Contribution from the Botanical Laboratory, University of Oklahoma, 40.

are quite distinct at a very early state—that there is neither arrest nor transformation during the ontogeny of the bud scale. In a recent paper Foster (1935) contributes information and evidence concerning the structure of the growing point, initiation of foliar primordia, comparative histogenesis and tissue specialization in the foliage leaves and bud scales of *Carya Buckleyi* var. *arkansana*. The present writer has nearly completed a similar study involving the bud scales, foliage leaves and stipules of the genus *Morus*, but unusual features concerning the bud scale have been found which seem to justify a preliminary description.

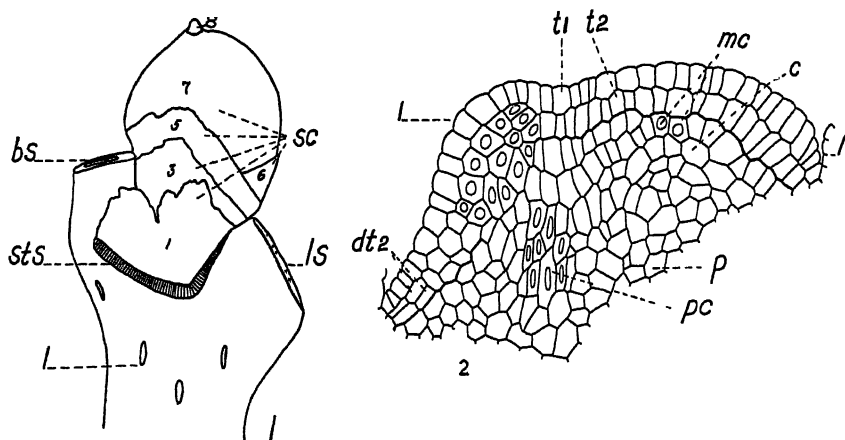


Fig. 1. Winter bud of portion of twig of *Morus alba*; *l*, lenticel; *sts*, stipule scar; *ls*, leaf scar; *bs*, terminal bud scar; *sc*, bud scales. $\times 8$.

Fig. 2. Median longitudinal section through stem tip and young leaf; *pc*, procambial tissue that will become the median leaf trace of the young leaf to the left; *p*, pith; *dt2*, cells derived from T-2, contributing to cortex of internode; *l*, foliage leaf initial; *t1*, outer tunica; *t2*, inner tunica; *mc*, initial cells of corpus; *c*, corpus; *l'*, older foliage leaf.

The histogenesis of the bud scale of *Morus alba* L. has been found to differ radically from Foster's account of scale development in *Carya Buckleyi* var. *arkansana*. The differences are of a fundamental nature and suggest the need of further researches involving additional genera. The present account is purely descriptive. No interpretations are made as it is intended for these to appear later in a paper dealing with comparative histogenesis of foliar structures in the genus.

THE SHOOT SYSTEM

The twigs of *Morus alba* are slender and cylindrical. At the base occur the narrow scars of from eight to eleven two-ranked bud scales. The leaf

scars occur in two opposite rows. Normally five or six of the latter appear, but this number may be greatly increased, especially in the case of coppice shoots.

The leaf scars are round, and are raised somewhat above the surface of the twig. The bundle traces, from eight to eleven in number, are scattered near the center of the scar. They protrude definitely above the surface of the scar. The stipule scars occur laterally at the level of the median portion of the leaf scar (fig. 1).

Axillary buds are present, all of which contain flowers. One or two smaller, accessory collateral buds usually accompany the main lateral bud. Terminal resting buds do not form. The apical meristem, with several young leaves in various stages of development, degenerates and usually drops from the twig at the end of the period of bud expansion in the spring. Since terminal resting buds do not form, there are but two growth periods associated with the formation of each shoot: during the first, the bud scales are formed; and during the second, the foliage leaves appear.

THE GROWING POINT

Hanstein's classification of tissues into dermatogen, periblem and plerome has been discarded by several recent workers including Schmidt (1924) Rösler (1928), Kühl (1933), Zimmerman (1928), and Foster (1935). It was shown by Schoute's (1902) researches and literature review that the Hanstein conception is not applicable to the growing points of all plants, and that the three classic histogens, even when present, are of little morphological significance. Schmidt (1924) suggested the terms "tunica" and "corpus" as substitutes for the terminology of Hanstein. He defined the tunica as the external layer or layers of cells at the stem tip which do not ordinarily divide in the periclinal plane except during leaf initiation. The corpus included all of the remaining internal tissue in which divisions may occur in any plane. The general applicability of Schmidt's conception has been discussed by Foster (1935) and need not be repeated here. The terms "tunica" and "corpus" as defined by Schmidt, will be used in this paper. While these terms represent tissues discrete at the growing point, they imply nothing concerning the origin of the vascular and cortical tissues of the stem.

Numerous median or nearly median longitudinal sections of the growing point of *Morus* suggest that the tip consists of a two-layered tunica and a central corpus (figs. 2, 4, 5). Foster (1935) found a similar situation in *Carya*, and for clarity in discussion referred to the outer layer of the tunica as T-1, the inner layer as T-2. Foster's scheme will be utilized in the present paper. T-1 (outer tunica layer) is homologous with the dermatogen of

Hanstein, while T-2 (inner tunica or subepidermal layer) corresponds to the perilem.

An idea of the structure of the growing point and the behavior of the histogens may be obtained by a study of figure 2, which is a section through

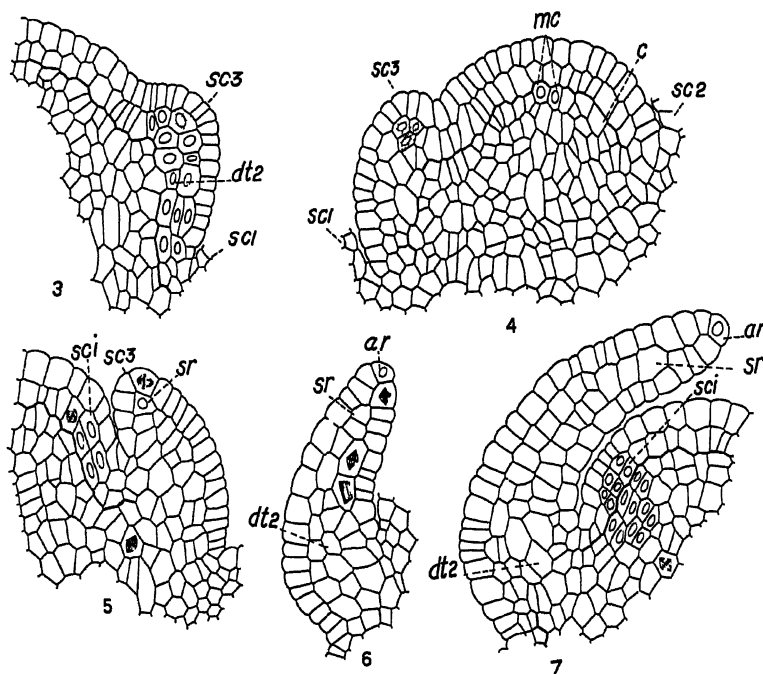


Fig. 3. Longitudinal section through portion of growing point and young bud scales; *sc3*, third scale (60μ high); *sc1*, first scale; *dt2*, inner derivative of T-2.

Fig. 4. Longitudinal section through stem tip and slightly older scales; *sc1*, first scale; *sc2*, second scale; *sc3*, third scale (70μ high); *c*, corpus; *mc*, initial cells of corpus.

Fig. 5. Longitudinal section through portion of stem and third scale (80μ high); *sc3*, third bud scale; *sc1*, initial of fifth scale; *sr*, subapical row.

Fig. 6. Longitudinal section of a fifth scale (110μ high); *ar*, apical row; *sr*, subapical row; *dt2*, derivatives of T-2.

Fig. 7. Longitudinal section of a fifth scale (150μ high); *ar*, apical row; *sr*, subapical row; *sc1*, initials of seventh scale; *dt2*, derivatives of T-2.

a stem tip that has been giving rise to foliage leaves. T-1 will be observed in every case as a discrete layer continuous over the stem tip and the young leaf at the left of the illustration. The independent origin and the exclusively anticlinal divisions of the cells of this layer are clearly evident. T-2 likewise occurs as a discrete layer, continuous over the stem tip beneath T-1, but at the left of figure 2 periclinal divisions in this layer have oc-

curred in connection with the formation of a young foliage leaf. Except during leaf or scale formation, periclinal divisions were never found in T-2 at the stem tip. In the internodal regions, however, periclinal divisions prevailingly occur in T-2, and the inner derivatives contribute to the cortex.

Beneath T-2 directly below the center of the stem tip in figure 2 will be observed a large pair of initial cells away from which the elements of the corpus diverge. From these large cells the outer one or two layers of the corpus may often be traced laterally to the base of the young leaf or bud scale, although periclinal and oblique divisions may occur at any time in the corpus, thus destroying the identity of the layers. It seems evident that the apical growth of the corpus is controlled largely by a pair or group of cells as evidenced by figures 2 and 4.

In some sections T-1 and T-2 seemed to diverge from respective groups of initials, but this behavior was not always evident as in *Carya*. In transection there may be frequently observed striking differences in size and staining reaction between the apical group of T-1 initials and the surrounding cells.

The activity of the corpus during foliage leaf initiation will be discussed in detail in a later paper. In figure 2, a procambial strand is forming to the left in the illustration, in the peripheral region of the corpus. This strand is formed in association with the young leaf, and will later become the median leaf trace. The trace differentiates basipetally until connection is established with the main vascular cylinder, and acropetally into the young leaf. Outside of the procambial strand the corpus gives rise to cortical tissue which will be augmented later between the nodes by derivatives of T-2. The central corpus becomes the pith.

THE INITIATION AND DEVELOPMENT OF THE BUD SCALE

The earliest evidence of bud scale initiation is shown by the appearance of periclinal walls in T-2 (figs. 5, 7). These walls first appear distinctly to the side of the growing point in the region that will later become the abaxial surface of the scale. In vertical section four or five cells finally appear to be active but this periclinally dividing layer in T-2 actually involves from one-third to one-half of the circumference of the growing point. The outer layers of the corpus also divide (fig. 7). Subsequent enlargement of the derivatives of the tunica and corpus results in the appearance of a bulge to the side of the growing point which in surface view appears as a crescent-shaped scale initial.

Figure 3 shows a longitudinal section of a portion of the stem tip and the third bud scale. For convenience a heavy dark line has been drawn to

delimit the tunica and corpus. The bulk of the young scale apparently consists of derivatives of T-2 which have enlarged considerably, although the corpus contributes slightly to the base of the scale. Near the abaxial surface one of the derivatives of T-2 has undergone a periclinal division; elsewhere only anticlinal walls have formed.

APICAL GROWTH OF THE SCALE

The method of growth of the scale immediately following the stage depicted in figure 3 may be seen by reference to figure 4. Near the tip of the scale in figure 3 is a dotted, subapical cell. In figure 4 this cell has apparently undergone two successive divisions—the first periclinal, the second anticlinal with respect to the surface of the primordium. Observations of many young scales indicate that divisions occur in this manner in nearly all scales and that subsequent increase in length is initiated by means of anticlinal divisions. In addition, the enlargement and division of the cells near the abaxial surface have resulted in a general increase in size of the young scale, and a decidedly greater curvature of the abaxial surface. The demarcation between the corpus and T-2 in the primordium is indistinct at this stage, but by carefully studying T-2 near the stem tip and by following this layer down into the young scale, it appears that the internal layers of cells of which the scale now consists have certainly been derived, mainly, if not entirely, from T-2. This contrasts with *Carya Buckleyi* where Foster found that the internal region of the young bud scale consists of a core of tissue derived from the corpus.

Following the stage represented in figure 4, anticlinal divisions occur in the cells near the tip of the scale. This results in a rapid increase in length, without however, an increase in radial thickness. In figure 5 is shown a longitudinal section of a bud scale in which such divisions have occurred. The increased length is due entirely to activity in the epidermal and subepidermal cells, which in turn, are derivatives of T-1 and T-2 respectively. Thus most of the scale shown in figure 5 may be safely referred in origin to the tunica, although a line delimiting the derivatives of the tunica and corpus can no longer be drawn.

Near the tip of figure 5 is a large, triangular subapical cell. This cell (a derivative of T-2) is a member of a subapical row which is continuous over the tip from one margin of the scale to the other. The function of the subapical row in the growth of the scale may be seen by reference to figures 6, 7 and 8, where, by transverse divisions, the row has given rise to a plate-like core of tissue enclosed by the young epidermis. This plate-like core, especially conspicuous in figure 8, is continuous at the tip between the margins of the scale.

In the epidermal layer at the extreme tip of the scale depicted in figure 6 is a large cell easily distinguished from its neighbors. The cell thus represented is a member of an apical row which extends over the scale tip, and is continuous with similar cells on either margin. The behavior of the apical row is apparent from figures 6, 7, and 8, where a series of divisions have occurred which simulate closely the divisions characteristic of the wedge-shaped marginal initials in the leaves of many leptosporangiate ferns (Bower, 1889). The initials of *Morus* are wedge-shaped and five-sided. They have two main cutting faces, but they occasionally divide in a plane perpendicular to the edge and to the surface of the leaf. Divisions are not confined to the apical row since mitotic figures frequently appear in its derivatives (fig. 6).

There is thus developed a scale which in median longitudinal section may be divided into four parts (figs. 6, 7): (a) a basal portion several cells in radial thickness, probably derived entirely from the tunica; (b) a median portion four layers of cells in radial thickness, certainly derived from the tunica; (c) a region near the apex consisting of three layers of cells, i.e. the epidermal layers and the derivatives of the subapical row; and (d) the apical region, consisting of the derivatives of the row of apical initials. The basal portion (fig. 7) shows the beginning of periclinal divisions in the abaxial subepidermal layer. Increase in radial thickness occurs partially as a result of such divisions, and partially as a result of similar divisions in the adaxial subepidermal layer. It is worthy of note that the basal portion of figure 7 is approximately 60μ in height, measuring from the juncture of the abaxial epidermis with the main stem to the region where the young scale is four layers of cells thick.

The scale now increases rapidly in length, by divisions in the apical row, the subapical row, the derivatives of these rows, the epidermis, and the region described above as four layers of cells thick. Anticlinal divisions resulting in an increase in length apparently do not occur in the basal region. Figure 8 is a median longitudinal section of a young scale which has attained a height of about 300μ . Although the total length of this structure is double that of the scale shown in figure 7, the length of the thickened basal portion is about the same in both cases. This indicates that the bulk of the scale is derived from the parts above the thickened basal portion as shown in figures 6 and 7, in other words from those regions which had their origin in the tunica at the growing point. It will be noticed in figure 7, that the abaxial half of the scale grows more rapidly than the adaxial, and as a result the scale curves protectively over the growing point. There is no indication of procambial tissue in either the scale or its subtended nodal region at this stage.

Apical growth of the scale continues in the manner described above until a height varying from 350 to 500 μ has been attained. At this time the apical row of initials, each member of which has functioned as an apical cell with two main cutting faces, experiences a change in mode of division.

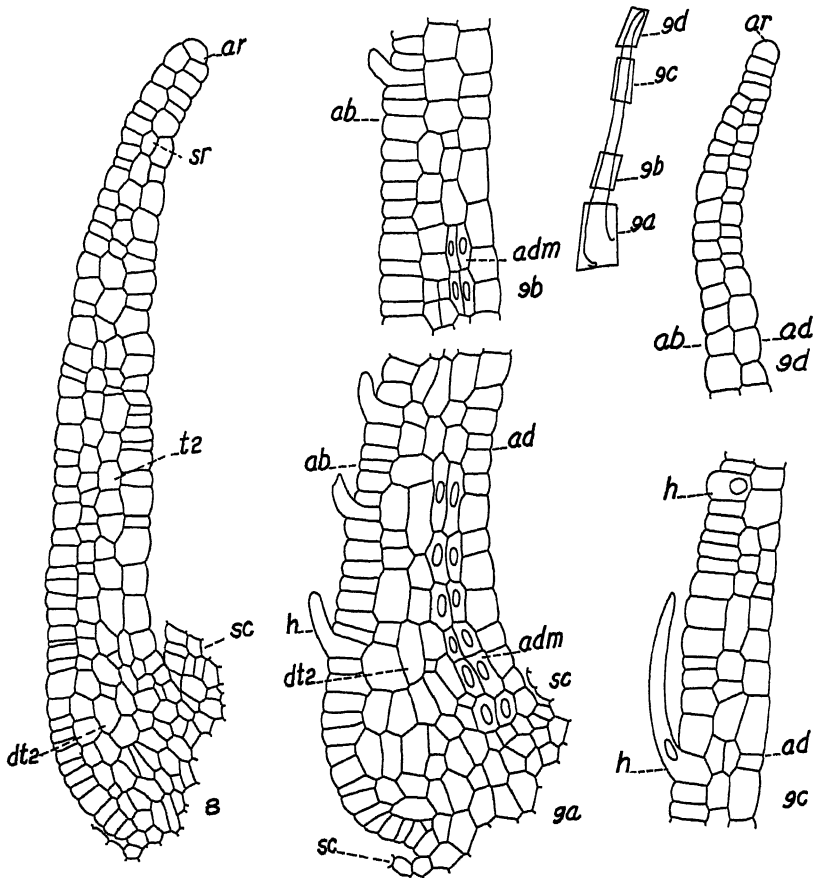


Fig. 8. Longitudinal section of a fifth scale (about 300 μ high); *ar*, apical row; *sr*, subapical row; *t2*, derivatives of T-2; *dt2*, probably derivatives of T-2.

Figs. 9a-9d. Longitudinal sections at various levels in a fifth scale (about 750 μ high); *sc*, scale; *dt2*, derivatives of T-2; *adm*, origin of adaxial meristem; *h*, hair; *ab*, abaxial surface; *ad*, adaxial surface; *ar*, apical row.

The new walls are laid down perpendicular to the longitudinal axis of the scale, and each member of the apical row produces a single chain of cells. The chains collectively form a sheet of tissue one cell thick at the apex (fig. 9d.) The amount of such tissue varies with individual scales. Since the apical row of initials is continuous with a similar row on each margin of the

scale, it might be expected that the marginal rows ultimately undergo similar changes in mode of growth, resulting in the formation of borders of tissue one cell thick which converge on the similarly constructed apex. Studies of cross-sections show this to be the case.

The basal portion of the scale (fig. 9a), i.e. the portion previously characterized as several layers of cells in thickness, gradually increases in length. This is due partly to the fact that its cells have enlarged, and to a limited extent, have produced new walls. However, the main way in which its limits have been extended is that periclinal walls have appeared in the internal layers of the region originally four layers of cells thick. The vertical extent of these periclinal walls is shown in figure 9a, where the divisions have occurred with greatest regularity in the adaxial subepidermal layer. The subepidermal dividing layer in figure 9a represents the origin of a cambium-like meristem, some of the derivatives of which later become the first vascular strands in the young scale. The periclinal divisions of the adaxial subepidermal layer gradually extend up the scale, and the region previously four layers of cells thick now consists of five layers (fig. 9b). In a similar manner periclinal walls occur in the median layer of the scale near the apex (fig. 9c). These walls usually appear near the center of the three-layered area and from this point are formed basipetally and acropetally (fig. 9c).

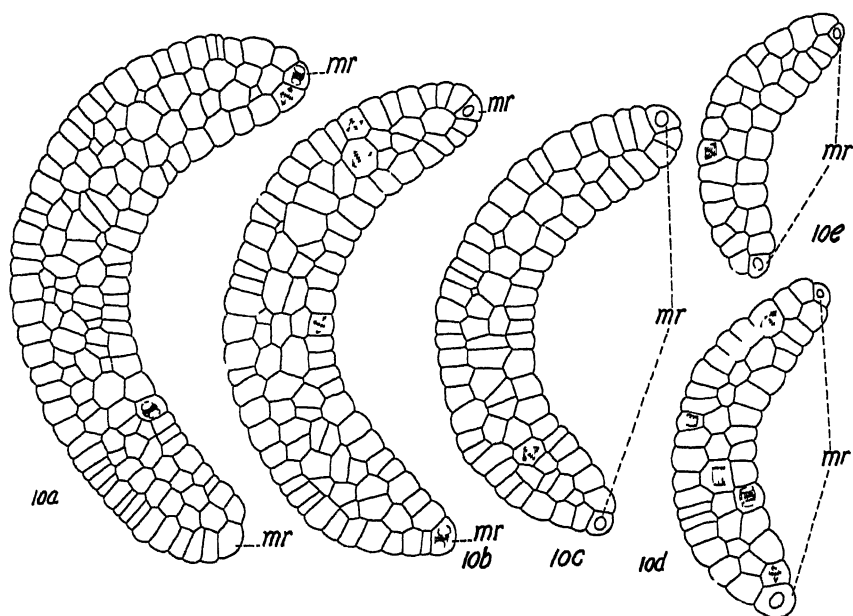
When the scale has reached a length of 500 to 600 μ most of the adaxial epidermis has begun to mature, and divisions in it occur only rarely. The abaxial epidermis, however, retains the ability to divide actively as evidenced by the smaller, columnar nature of the cells, and by their dense protoplasmic contents. Numerous unicellular hairs are produced by the abaxial epidermis, a phenomenon which as suggested by Foster (1935) for *Carya* may be correlated with their active meristematic qualities. The hairs first appear near the median portion of the lower epidermis, but the area of their occurrence rapidly extends basipetally, acropetally and laterally. At maturity these hairs become quite stiff and appressed.

MARGINAL GROWTH OF THE SCALE

The method by which the young scale increases in width is practically identical with its mode of increase in length. Because of the tendency of the scale to curve over the apex of the stem, it is impossible to obtain perfect cross-sections of very young stages (figs. 4, 5). As growth proceeds, however, the scale becomes nearly erect due to the expansion of younger foliar organs, so that it was possible to obtain nearly perfect cross-sections of the 100–120 μ stages.

Figures 10a–10e represent a series of cross sections of a scale approxi-

mately 120μ high. Reference to figure 10a reveals that the basal portion is nearly twice as broad as the scale is high. The lower margin is occupied by a large cell, somewhat similar in appearance to the cell seen at the apex of figure 6. The opposite (upper) margin is occupied by another such cell which is in the process of division. It is apparent that the new wall is being produced at such an angle that one of the daughter cells will resemble the

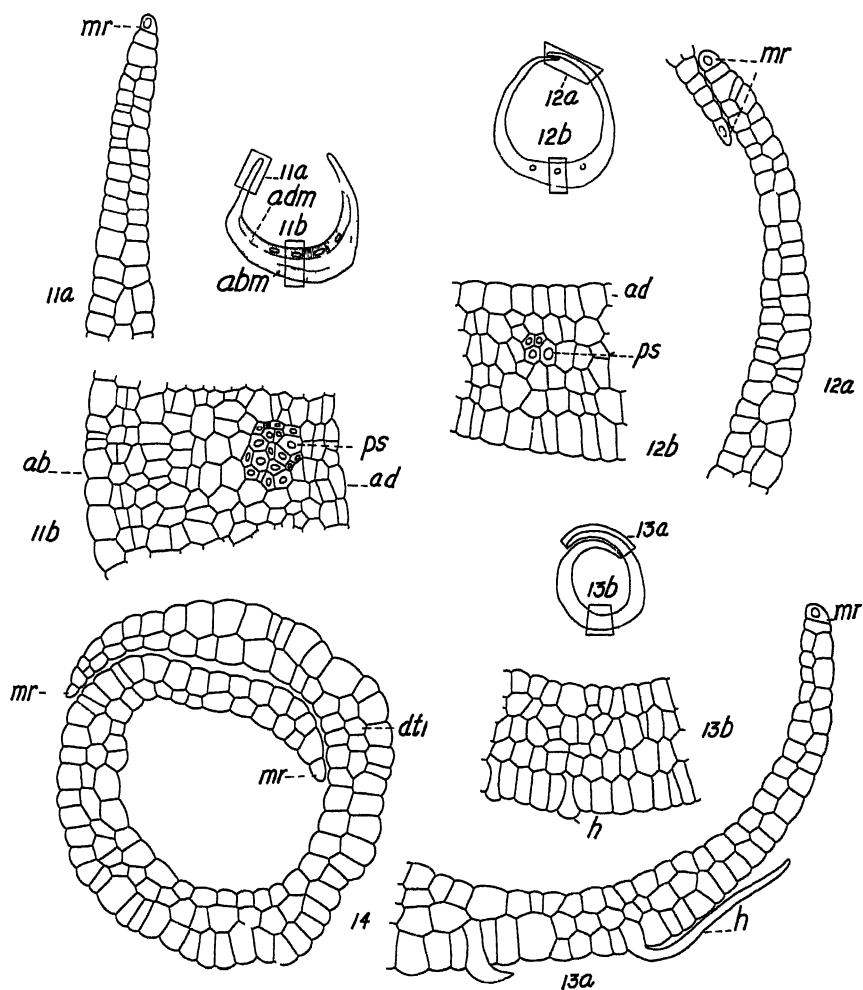


Figs. 10a-10e. Transverse sections at various levels of a third scale (about 120μ high); *mr*, marginal row.

wedge-shaped apical initials found at the scale tip. Twenty-five microns above figure 10a, and from there on to the tip of the scale, both margins possess well differentiated marginal initials (figs. 10b, 10c, 10d, 10e) which become continuous with the apical row. Thus the entire edge of the scale, from the base of one margin over the tip to the base of the other consists of a continuous row of wedge-shaped initials which adds to the width and height of the scale.

Immediately beneath the surface initial on each margin (fig. 10a) will be seen a large cell, clearly a derivative of T-2. Studies of serial sections (figs. 10b, 10c, 10d, 10e) show that such cells are members of submarginal rows which converge on the subapical row at the apex. The submarginal rows contribute to marginal growth in the same manner that the subapical row increases the vertical extent of the scale.

Since the submarginal and subapical initials of the scale primordium, in addition to the region previously described as four cells thick, may be traced in origin to the outer derivatives of T-2 (fig. 3), one may safely con-



Figs. 11a-11b. Portions of a transverse section about 20μ above the base of a fifth scale (about 850μ high); *ab*, abaxial surface; *ad*, adaxial surface; *ps*, procambial strand; *mr*, marginal row; *abm*, abaxial meristem; *adm*, adaxial meristem.

Figs. 12a-12b. Portions of a transverse section about 120μ above base of scale shown in figures 11a and 11b.

Figs. 13a-13b. Portions of a transverse section about 250μ above base of scale shown in figures 11a and 11b; *h*, hair.

Fig. 14. Transverse section about 500μ above base of scale shown in figures 11a and 11b; *dtl*, derivative of T-1; *mr*, marginal row.

clude that most of the scale, probably all of it, is to be regarded as a derivative of the tunica. However, since the demarcation between the tunica and corpus becomes indistinguishable at an early stage (figs. 4, 5) the possibility cannot be discarded that the corpus contributes slightly to the basal region.

As the scale increases in width walls laid down by the marginal initials gradually become perpendicular to the surface of the scale. When this occurs the marginal initials produce a narrow plate of tissue one cell thick (figs. 11a, 12a, 13a, 14). Divisions of this type in the marginal row occur later in the ontogeny of the scale than do the similar divisions in the apical row. In figure 11a the derivatives of the marginal row are plainly visible, first as a double layer and finally as a single layer of cells. The continuity of the double and single layers can be proven by a study of figures 11a, 12a, 13a, and 14, which are cross-sections at various levels of a scale about 650μ high. The continuity of the layers over the apex can be established by referring once more to figure 9d. At the 750μ stage the scale may be visualized as having an outer fringe of tissue one layer of cells thick and an inner area two layers of cells thick, both of which are continuous from just above the base of one margin over the apex nearly to the base of the other. The type of marginal and apical growth exhibited by *Morus* during late stages of scale development differs markedly from that described for *Carya* by Foster (1935). The scale of *Carya* grows in length and width in its early stages by the activity of subapical and submarginal groups of initials, augmented by the derivatives of more or less independent groups of dividing cells which are scattered throughout. This naturally results in the production of a much more bulky scale in *Carya*.

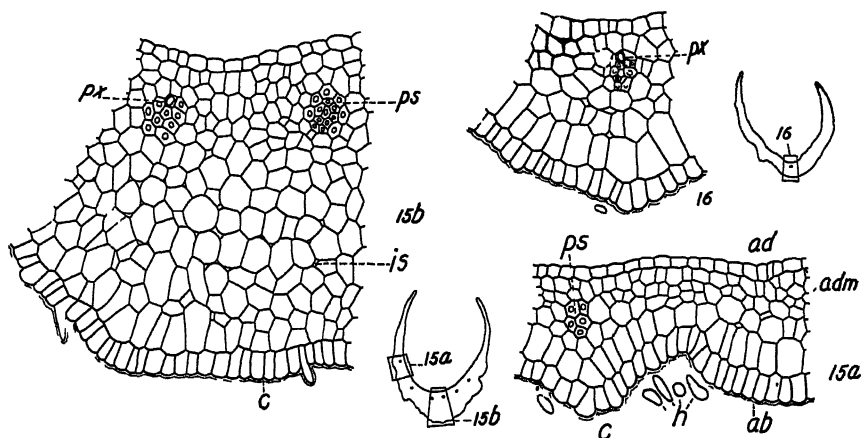
GROWTH IN RADIAL THICKNESS

Localized growth in radial thickness is initiated in the basal region when the scale is from 500 to 700μ in length, although occasional periclinal divisions occur from the beginning in the abaxial subepidermal layers (fig. 3). Increase in thickness is achieved through the cambium-like activity of both the ab- and adaxial subepidermal layers (fig. 11b). The adaxial layer is first involved, near the median, basal region, but the divisions rapidly spread both acropetally and laterally. Derivatives of the adaxial meristem contribute largely to the first formed vascular strands. These are initiated very late in the basal part of the scale (fig. 11b), differentiate acropetally and basipetally, and fuse irregularly in the cortex of the trilacunar node. Later, isolated strands appear farther up in the scale (fig. 12b), which differentiate acropetally and basipetally until they become continuous with the previously formed strands of the basal portion.

The scale is increased in thickness in the distal portions by periclinal division of the abaxial epidermal layer. Such divisions, however, occur

irregularly and produce isolated areas three layers of cells thick (figs. 13a, 14). Periclinal walls were never found elsewhere in the epidermal or T-1 layers.

The extent of meristem formation in the abaxial subepidermal layer varies with individual scales. The first four or five scales formed, grow considerably in this manner and have radially thickened basal portions. The inner scales, however, do not have conspicuously enlarged bases, and the activity of the meristems is reduced accordingly.



Figs. 15a-15b. Portions of a transverse section about 250μ above the base of a third scale (about 1000μ high); *is*, intercellular space; *c*, cutin; *px*, protoxylem element; *ps*, procambial strand; *adm*, adaxial meristem; *h*, hair.

Fig. 16. Portion of a transverse section about 510μ above the base of the scale shown in figures 15a and 15b.

Figs. 2-14 drawn at table level with Spencer camera lucida, under 2 mm. Leitz apochromatic objective, with periplan ocular $8\times$; reduced to one-fourth original size. Height given for young scales is the distance from the scale tip to the juncture of the abaxial surface and the main stem.

Figs. 15-16. Drawn and reduced as above, except with the use of a 4 mm. Leitz apochromatic objective.

The very late differentiation and maturation of vascular tissue are of interest since in these features the scales of *Morus* present a striking contrast with the situation in *Carya*. No trace of procambium was found in fifth scales up to 750μ high, and the first mature xylem elements were found in scales about 1000μ in height (figs. 15b, 16). In *Carya*, however, Foster found procambial tissue in the base of a scale 72μ high (op. cit. fig. 19a).

Detailed studies of the maturation of the scales were not made. In general this phenomenon is accompanied by the enlargement and vacuolation of all cells, particularly those in the abaxial portion (figs. 15a, 15b, 16). Intercellular spaces are conspicuous in scales 800μ high. A fully ma-

ture bud scale usually has from thirty-six to forty parallel, independent veins.

The walls of the epidermal cells thicken, and a layer of cutin is deposited over the abaxial surface. Stomata are formed in the abaxial epidermis. The cells of the abaxial subepidermal layer elongate in a plane perpendicular to the surface (figs. 15a, 15b), and in areas exposed to the air, become suberized.

During bud expansion in the spring, all of the scales except the outer four or five, elongate considerably and become photosynthetic. The elongation is achieved by cell division, particularly in the adaxial regions, and by cell enlargement. Although latex canals occur constantly in foliage leaves, they were not found in bud scales of any age.

SUMMARY

1. The growing point of *Morus alba* consists of a two-layered tunica and a central corpus. For convenience the outer tunica layer is called T-1, the inner T-2.

2. The bud scale is initiated by periclinal divisions in T-2 and the outer corpus. Most of the scale is derived from the tunica, but the corpus apparently contributes slightly to the basal portion.

3. Early in the ontogeny of the scale there is formed: (a) a bulky basal region, derived mainly from the tunica, but perhaps partly from the corpus; (b) a region four layers of cells in radial thickness, derived from T-1 and T-2; (c) a subapical row of initials derived from T-2; (d) a submarginal row of initials beneath each edge of the scale, derived from T-2, and converging upward to the subapical row; (e) an apical row of initials derived from T-1; (f) a marginal row of initials derived from T-1 and converging upward to the apical row.

4. All of the adult scale except a small median basal portion consists of derivatives of the apical row, marginal rows, subapical row, submarginal rows, and the region four cells in thickness. The original bulky base, the exact origin of which is somewhat in doubt, contributes little or nothing to the scale's apical and marginal growth. Thus the entire scale, with the possible exception of a basal portion is a product of the *tunica*.

5. The activity of the apical and marginal initials is strikingly suggestive of the mode of growth common in the young lamina of leptosporangiate ferns.

6. Vascular tissue differentiates very late, when the scale is 800–900 μ in height. It forms as isolated strands which differentiate acropetally and basipetally.

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Germination of the resting spores of *Diplophlyctis intestina*

J. S. KARLING

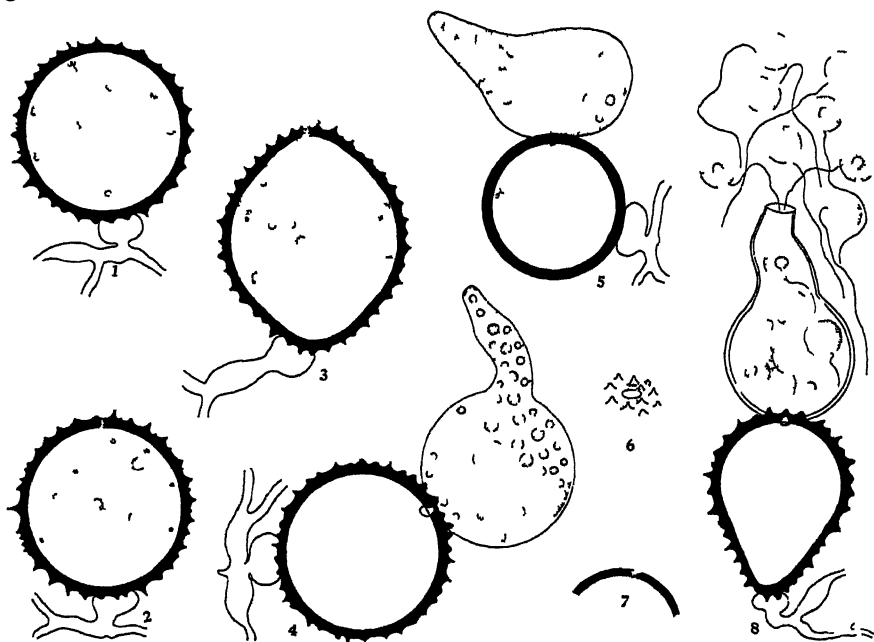
(WITH EIGHT TEXT FIGURES)

Since the time *Diplophlyctis intestina* (Schenk) Schroeter was first discovered by the author in species of American Characeae in 1928, continual observations have been carried on to determine the method of germination of its resting spores and to complete our knowledge of the life history of this chytrid. Such spores occur in great abundance in dead nodes and internodes of *Chara*, *Nitella*, and other stonewort genera, and as has been proven experimentally serve as sources of infection from disintegrated host tissue. Yet in spite of this evidence, and extensive attempts to induce germination by freezing, heating, drying, etc., the results have been largely negative. Occasional isolated and empty spore cases with adhering vesicles have been seen from time to time, but because of their scarcity and the fact that no progressive developmental stages were found the author has been hesitant in describing and reporting the observed phenomena as universal and characteristic for this species. However, on New Year's Eve, 1935, myriads of resting spores in all successive stages of germination were found for the first time, and the process could be followed with comparative ease in the living material. Since that time germinating spores have been found almost at will, primarily because of familiarity with the appearance of the developmental and mature stages, and these subsequent observations have confirmed in every detail those made on New Year's Eve.

What the special environmental conditions were which led to such widespread germination at that time has not been determined. The *Nitella flexilis* filaments in which the resting spores developed had previously been killed by immersion in hot water for an hour, inoculated and allowed to stand in a small battery jar on a table near an eastern window in the laboratory. Within four days most of the algal filaments became heavily infected, and after a week resting spores were present in great abundance. Germination occurred approximately a month later. During this time the morning sunlight frequently fell directly on the culture for a few hours, and in the course of the nights the temperature in the laboratory often dropped below 50°F. during December. The culture was thus subjected to varying degrees of temperature and light intensity. Subsequent observations have led the author to believe that germination is rather common under ordinary laboratory conditions, and that such an environment is fairly optimum. Furthermore, the data at hand suggest, at least, that under such conditions the spores germinate very shortly after maturing, without

any prolonged resting period. Whether or not there is a definite periodicity out-of-doors has not yet been ascertained.

As has already been described by Zopf (1884), Sparrow (1932) and myself (1928) the majority of resting spores have a thick, brown, warty or spiny outer wall, although occasional smooth ones may be found. Whether or not the latter character is specific and we are dealing with more than one species has not been definitely determined. The content in the resting state is usually coarsely granular, with the granules and globules of such size and abundance and so closely crowded together that



Figs 1-8 Successive stages in the germination of the resting spores of
Diplophlyctis intestina

many of the spores frequently appear as if they had undergone cleavage into segments. The first marked visible change in germination is the gradual breaking up of these granules into successively smaller units, and their dissolution. As this goes on the remaining ones appear more and more separated, and it soon becomes apparent that they are embedded or suspended in a more or less optically homogeneous hyaloplasm. Figure 1 shows a comparatively early stage in which smaller granules or globules appear to have been split off from the larger ones and lie between them. These bodies decrease in size and number with the successive germination stages, figure 2, and at the same time the remainder of the protoplasm becomes more finely granular and hyaline.

Concurrent with these changes a comparatively small cylindrical opening or pore develops in the thick outer wall. This opening is usually quite small and varies only slightly in size, so that it may be readily overlooked in living material before the spore content begins to emerge. So far I have been unable to follow the stages of its development because of the thickness and opacity of the cell wall. It may occur at almost any place on the periphery of the spore, and in one instance it was found at the point of attachment of the apophysis. Figures 2, 3 and 7 show the pore in longitudinal section, while in figure 6 it is shown in surface view. Sometimes it may be wider on the outer surface and appear somewhat funnel-shaped; at other times oval. So far only a single germination pore has been found for each individual spore.

In figure 2 is shown a median longitudinal view of a spore in which the content is beginning to emerge. The emerging vesicle appears to be quite naked at this stage, and in general appearance it seems to be more or less hyaline or finely granular with a few minute suspended refractive globules. Whether or not it is surrounded by a definite membrane at this stage is difficult to determine in living material. A later stage is shown in figure 3 in which approximately half of the content has emerged. In this figure the suspended, hyaline, refractive globules are more numerous and somewhat larger. This difference, however, is hardly to be regarded as a developmental change, since the appearance of the bodies varies considerably in different spores in the same stage of germination. Sometimes the protoplasm at this stage contains a number of vacuoles, similar to those of the developing evanescent zoosporangia; but from observation of numerous cases I have come to regard extensive vacuolation as frequently concomitant with degeneration. As the protoplasm flows out and draws away from the wall of the spore, irregular granules, hyaline globules and other residue may frequently be left behind, as is shown in figures 3 and 5.

Gradual emergence of the protoplasm continues until the entire content of the resting spore has escaped to form a vesicle on the outside. This vesicle then becomes transformed into a zoosporangium. Figure 4 shows a comparatively late stage in which the zoosporangium has been completely formed. It possesses a definite wall and a large exit tube or sporangial neck, and contains a definite number of large spherical, refractive globules suspended in a finely granular and more or less hyaline background. The maturation of this sporangium is essentially similar to that of the evanescent zoosporangia formed earlier in the life cycle of this organism. The refractive globules seem to originate by individual increase in size and confluence of smaller droplets, and process of spore delineation is by progressive cleavage. As to shape these zoosporangia vary from

spherical to oval, tubular, elongated and slightly irregular. As a general rule, however, they do not show the same range of variation in size as the earlier evanescent zoosporangia. Their size is more directly proportional to that of the resting spore from which they are formed. The exit tube also varies in diameter and length, but it does usually grow to the extreme length that may frequently be found in the evanescent sporangia.

The zoosporangium shown in figure 4 is mature and ready to undergo cleavage. This process is distinctly progressive and not simultaneous. In sporangia lacking a large central vacuole the cleavage furrows generally begin at the periphery and progress inward, but when a vacuole is present they also may begin in the center and travel outward. These furrows orient themselves in such a manner that each segment or zoospore initial at maturity contains only one of the large hyaline, refractive globules, as is shown in figure 5. Shortly after cleavage is complete the tip of the exit tube bursts and the zoospores begin to emerge one after another (fig. 8). Their emergence, behavior, size, shape and structure are strikingly like those of the zoospores from the earlier evanescent sporangia. They are spherical, possess a single cilium posteriorly attached, a large refractive globule, and dart about with great rapidity. After a motile period varying from approximately thirty minutes to an hour and a half they gradually become quiescent, lose their cilium and germinate. A large percentage of them, however, may degenerate if conditions are not optimum for growth. Numerous germination stages have been observed, and this process also is similar to that of the earlier zoospores, as has been previously described by the author (1930). A germ tube is formed which penetrates the host cell wall and branches very shortly. These initial branches are the rudiments of the rhizoidal system, and as soon as it has been established an enlargement of the germ tube above the branches occurs. This is the *anlage* of the zoosporangium, and as it begins to increase in size another swelling is formed between it and the rhizoids, which eventually becomes the apophysis. As a result of this growth and differentiation the rhizoidal system becomes oriented on the apophysis immediately beneath the incipient zoosporangium. With subsequent development and maturity, the evanescent zoosporangium with uniciliate zoospores is formed.

It is obvious from the above description that germination of the resting spore of *Diplophlyctis intestina* is essentially like that of *Polyphagus Euglenae*, described by Nowakowski (1877b), Dangeard (1900) and Wager (1913), and that the spore as far as we know at the present time is fundamentally a cyst and prosperangium. Whether or not it is a zygote formed as the result of the union of two gametes has not been definitely determined. In my cultures of *Diplophlyctis* separate sporangia-bearing micro- and macrozoospores frequently occur, but fusion has not yet been ob-

served. In view of the increasing evidence for the widespread occurrence of heterothallism the natural assumption would be that they are male and female thalli and that the resting spore is a zygote, but until actual fusion has been observed this conception is purely hypothetical.

Our knowledge of the complete life cycles of the majority of rhizidiaceous chytrids is quite meager. In a large number of genera and species resting spores have never been found and in those where such structures are reported to occur very few germination stages have been observed. In the family Rhizidiaceae, to which our species belongs, germination of the resting spores has been reported, as far as I am aware, in only six other genera and species, including *Polyphagus Euglenae*, *Entophlyctis Vaucheriae* (Fisch, 1884), *Rhizidium mycophilum* (Nowakowski, 1877a), *Chytridium olla* (De Bary, 1887), *Zygorhizidium Willei* (Loewenthal, 1905), and *Rhizophidium ovatum* (Couch, 1932). In all these species with the exception of the last two the resting spore has been shown to function as a cyst of prosporangium, and germinates as in *Diplophlyctis intestina*.

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Five-leaflet poison oak

JAMES B. MCNAIR

(WITH TEXT FIGURES)

Five-leaflet poison oak (*Rhus diversiloba* T. & G. forma *quinquifolia* forma nova) (foliis 5-foliolatis) was not known to Torrey and Gray (1838) at the time that they first named the plant *Rhus diversiloba*. The first appearance of the plant in scientific literature is in 1890 in Brandegee's report of the plants of Santa Catalina Island.

To determine if 5-leaflet specimens had been collected previous to 1890 inquiries were sent to the following herbaria: the University of California, Berkeley, California; Pomona College, Claremont, California, (P); Los Angeles Museum of History, Science and Art, Los Angeles, California; University of California at Los Angeles, Los Angeles, California; University of Southern California, Los Angeles, California, (U. S. C.); Natural History Museum, San Diego, California; California Academy of Sciences, San Francisco, California (S. F.); Santa Barbara Museum of Natural History, Santa Barbara, California; Dudley Herbarium, Leland Stanford Jr. University, Stanford University, California; National Museum of Canada, Ottawa, Canada; University of British Columbia, Vancouver, Canada (B. C.); United States National Herbarium, Washington, D. C.; Field Museum of Natural History, Chicago, Illinois (F.); Gray Herbarium, Cambridge, Massachusetts; Missouri Botanical Garden, St. Louis, Missouri (M.); New York Botanical Garden, New York, N. Y. (N. Y.); Oregon State College, Corvallis, Oregon (O.); Academy of Natural Sciences, Philadelphia, Pa.; State College of Washington, Pullman, Washington; University of Washington, Seattle, Washington; and Rocky Mountain Herbarium, University of Wyoming, Laramie, Wyoming. As a result of this correspondence 5-leaflet specimens have been located as follows:

California: "Throughout California" 1866, *A. Wood* (N. Y.); Little Chico Creek, Butte Co., April 1896, *Mrs. R. M. Austin No. 749* (M.); Santa Catalina Island, August 1922, *E. C. Knopf* (F.); N. E. side Moraga Ridge, Oakland Hills, Contra Costa Co., Nov. 1, 1925, *John Thomas Howell No. 1541* (S. F.); Big Tujunga Canyon, just below and east of dam, alt. 2500 ft., May 13, 1934, *J. B. McNair* (U. S. C.); Cobal Canyon C. C. C. Camp, alt. 1500 ft., spring 1935, *J. B. McNair* (P); Corvallis, Oregon, Oct. 1935, *Helen M. Gilkey* (O). The writer first noticed 5-leaflet poison oak along the Mt. Wilson trail north of Pasadena, January 5, 1917. Observed by the writer along trail 200 yds. below Opid's Camp, West Fork San Gabriel R., alt. 4200 ft. Dec. 8, 1935.

A VEGETATIVE OR ECOLOGICAL FORM?

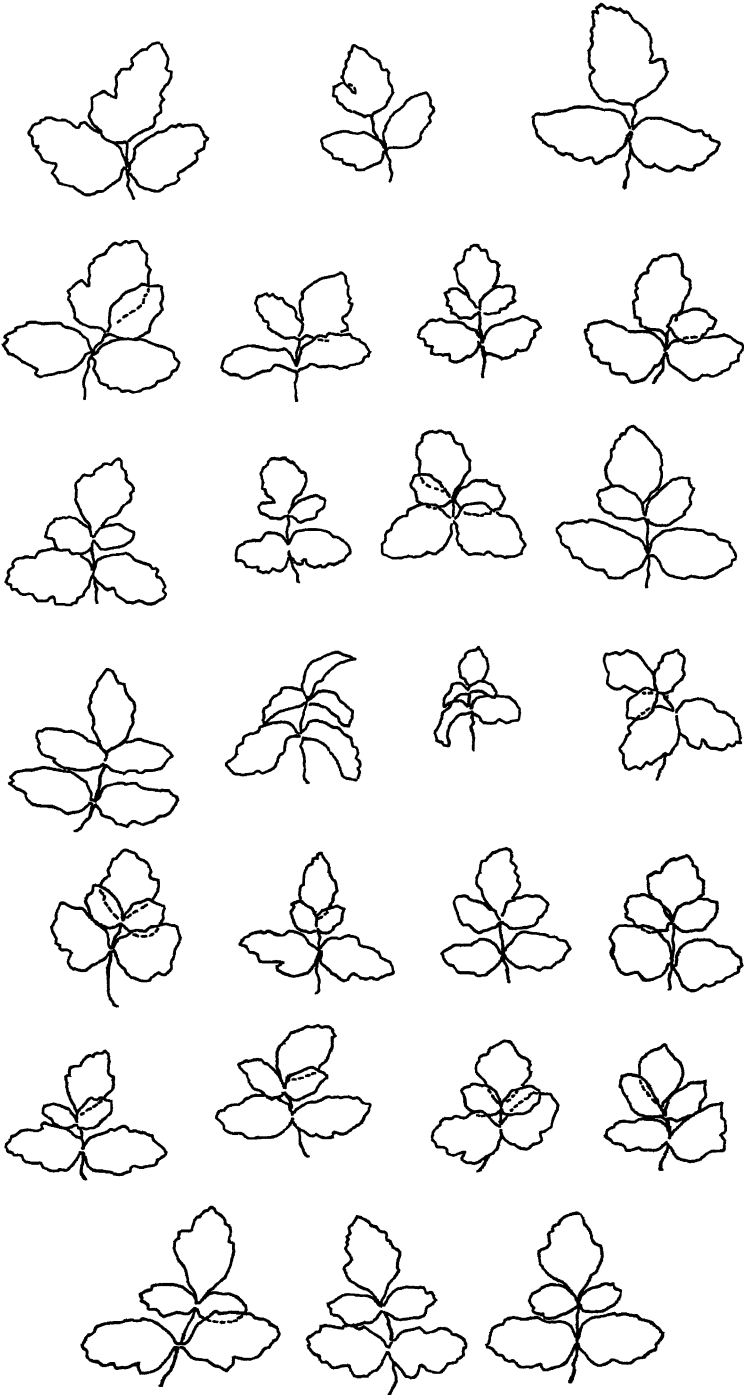
The question arises as to whether 5-leaflet poison oak is a vegetative or ecological form. The author cannot say what kind of soil or other conditions surrounded the specimens not observed nor collected by himself. But where he has observed these plants, plants of the 3-leaflet poison oak were found in the same localities. The author has found it only along the side of roads, trails or firebreaks. And in every case the plants on which the 5-leaflets are found have been cut back to their roots in an effort to kill them. In other words these plants may be considered as hedge or coppice forms produced by vigorous rapid growth. The conditions which bring about this 5-leaflet formation are therefore not ecological but vegetative. The plant consequently is a vegetative form. It seems best in order to prevent confusion with other plants to give this plant distinction as a form, *i.e.*, *Rhus diversiloba* T. & G. forma *quinquifolia*.

PHYLOGENY

A study of the plants which produce 5-leaflets shows that some of the plants have also 3- and 4-leaflet leaves as well as the 5-leaflet leaves. Some of the 3-leaflet leaves have very deeply incised lobes showing a marked tendency to form 4 and 5 leaflets as shown in text figures 1, 2 and 3. This tendency is no doubt caused by the increased vigor or energy of the plant due to pruning or cutting it back to the roots in an effort to destroy it. This supposition coincides with that morphological indicator of phylogeny compiled by Bessey (1915) which states that "simple leaves are more primitive than compound leaves." Or one can make a corollary under it to the effect that compound leaves with three leaflets are more primitive than compound leaves with more than three leaflets. This is shown not only in the case of 5-leaflet poison oak but in another one of the poisonous *Rhus*, namely *R. verniciflua* Stokes (*R. vernicifera* DC.). Mobius (1899) found that in the sprouting seeds of this plant 3-leaflet leaves were first formed, to be followed by the usual compound leaves of 11-15 leaflets. Therefore, as ontogeny is a brief recapitulation of phylogeny (Haeckel, 1906) we may say that in the poisonous *Rhus*, at least, the tri-foliolate plants precede in evolution the plants with compound leaves which produce more leaflets such as the 7-13 leaflet *Rhus Vernix* L. (poison sumach).

Grateful appreciation is extended to the curators of the various herbaria who have assisted in this study by sending data.

Text figs. Outlines of 3-, 4- and 5-leaflet leaves of *Rhus diversiloba* T. & G. all collected August 13, 1935 by V. McAlmon and J. B. McNair at Cobal Canyon mouth, Claremont, Cal. $\times 1.5$.



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Wound responses of *Ficus australis*

JOHN AUSTIN JUMP

(WITH SIX FIGURES)

Upon reviewing the literature on wound reaction and cicatrization of leaves, one gathers the impression that a leaf subjected to a traumatic stimulus will give a constant type of reaction if the conditions under which the experiments are performed are identical. Working with leaves of *Ficus australis* Willd. (*Ficus rubiginosa* Desf.) the writer has observed a number of variations in response, even in the same wound.

The outstanding publications on cicatrization prior to 1930 have been reviewed by Wylie (1930). The writer wishes however, to briefly mention certain papers that have a specific bearing upon this investigation. Massart (1898) notes that in foliar wounds on *Clivia miniata* Regel the neighboring cells proliferate and completely repair the wound. *Nuphar luteum* Sibth. & Smith was found to react by filling the large lacunae with proliferated cells in the vicinity of the wound. Gertz (1918) is reported by Wylie to have observed a marked hypertrophy of mesophyll cells bordering the tunnels of leaf miners. Blackman and Mathaei (1901) in an extensive investigation upon the wound reactions of *Prunus laurocerasus* L., find that the usual cicatrice is not formed when the material is kept moist in a beaker. Buscalioni and Muscatello (1911) were apparently the first to work with *Ficus australis*, but do not report the results that the writer has observed. Their paper is chiefly remarkable for the variety of methods which they employed in wounding many of the species which they enumerate. Krieger (1935) called attention to mesophyll proliferation and hypertrophy in *Ficus australis* but made no detailed study of it.

An understanding of the normal anatomy of the leaf of *Ficus australis* is necessary for the interpretation of wound reaction (fig. 1). The upper epidermis is multiple and heavily cutinized. The hypoderm consists of a layer of very large parenchymatous cells, one to two layers in thickness, in which occur idioblasts containing cystoliths. These idioblasts usually greatly exceed the normal hypodermal cells in size, and may be so large as to crowd out the layers of palisade immediately beneath. The palisade is double and contains numerous tanniniferous idioblasts which are usually confined to the upper and more compact layer of the palisade. The spongy tissue is very loosely organized and has large intercellular spaces. Tannin and latex occur in the spongy tissue, usually being found in more or less isodiametrical cells. Vascular structures show considerable variation, but the collateral bundle seems to be the most typical. Beneath the spongy tissue there is a low palisade, one cell in thickness, and a double layer of

cells composing the epidermis. The outer layer of this epidermis is composed of cells which are smaller and have thicker walls than those of the inner layer and is heavily cutinized. Stomata were found exclusively in the lower epidermis and sunken stomata are occasionally found.

The leaves upon which this study is based were wounded by cuts 4-12 mm. in length, using a sharp razor. The plant was approximately six years of age and grew in an unshaded position in one of the greenhouses of the University of Pennsylvania. The wounding was done during the late fall and winter months, and the leaves were allowed to remain upon the plant until collected for fixation. Material was fixed in Cohen's VIIc fixing fluid (1935) and stained in safranin and light green.

A few of the sections showed a definite cicatrice and pseudo-cicatrice, but in many cases a cicatrice failed to develop. In the latter instances the pseudo-cicatrice was usually either lacking entirely or only partially developed, and hypertrophied spongy tissue filled the intercellular spaces. As the proliferation of the spongy tissue continues, the new tissue fills the space caused by the wound and the surfaces of the wound are again organically united (fig. 3). In some cases one surface of the wound proliferates as described above, while the opposite surface cicatrizes (fig. 4).

When a cicatrice is not formed, the first reaction is the proliferation of cells in the spongy tissue. These cells are frequently hypertrophied and filled with granules of various size (fig. 2). The microchemical tests employed by the writer in attempting to determine the nature of these granules tended to indicate that they were derived from one of the constituents

Explanation of figures 1-6

KEY TO LETTERING

ci, cicatrice; *cu*, cell from spongy tissue becoming cutinized; *cy*, cystolith; *dl*, dead tissue; *hd*, hypoderm division; *l*, latex cell; *ps*, pseudo-cicatrice; *ti*, tanniniferous idioblast; *x*, cells containing granules of undetermined nature; possibly a constituent of latex.

Fig. 1. Normal leaf structure.

Fig. 2. Beginning of proliferation of spongy tissue following wounding.

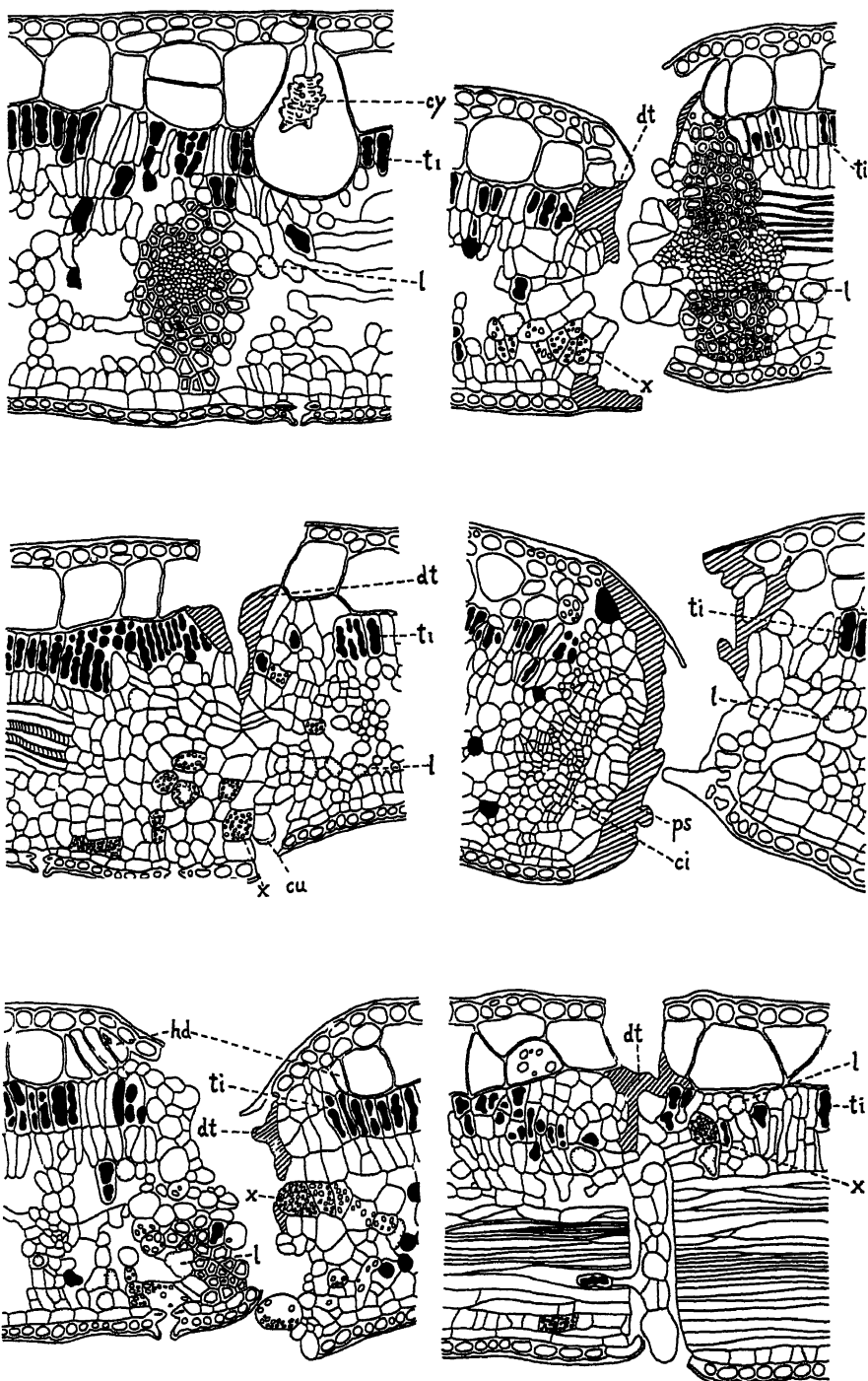
Fig. 3. Union of wounded surfaces. One of the cells of the spongy tissue in the region of the epidermis has secreted cutin on one side.

Fig. 4. Normal cicatrization on left surface of wound. Proliferation of cells with only a small amount of dead tissue on the opposite surface.

Fig. 5. Wounded section showing hypoderm becoming meristematic.

Fig. 6. Wound severing vascular bundle, showing spongy tissue filling the space between the cut ends of the bundle.

The sections illustrated in Figs. 2, 4, and 5 are all from the same wound and were fixed 32 days after wounding.



of the latex. The above reactions may begin within five days of wounding and continue for three weeks or more, until the wound is closed. The spongy tissue often proliferates so vigorously that it fills the space between the wounded surfaces ordinarily occupied by the palisade and hypoderm. Both of these latter tissues, however, were observed becoming meristematic in a few cases (fig. 5). This suggests that if the growth of the spongy tissue did not ordinarily proceed so rapidly, and insert itself between the opposite hypoderms and palisades, we might expect in some cases a more complete restoration of the original leaf structure. There was no evidence in this study of any tendency of the outer epidermal layers to become meristematic. There is, however, an attempt at a restitution of the epidermis by certain cells derived from the spongy tissue. In several cases it was noted that a mesophyll cell which had grown out into the plane of the epidermis apparently became cutinized, preparatory to functioning as an epidermal cell (fig. 3). In cases in which the wound severed xylem elements, the intervening space was promptly filled with cells derived from the spongy tissue (fig. 6).

The cause for these diverse reactions has not definitely been determined. It is apparent that if the razor does not make a clean cut there is considerable cell disintegration, usually resulting in a pseudo-cicatrice and cicatrice. This latter reaction also occurs if the leaf is young; the edges of the wound, in such cases, tending to gape excessively. When a mature leaf is wounded the cut surfaces tend to remain close together and usually become partially sealed by the latex which exudes abundantly and then dries. This may in part account for the absence of any great amount of cell disintegration on the part of the cells bordering the wounded surfaces. However it is still necessary to account for the cases in which one of the wounded surfaces proliferates abundantly without cicatrizing, while the opposite one forms a cicatrice and pseudo-cicatrice. In most instances in which this occurred, the surface which cicatrized was found to have been cut off from its nearest food supply by the wound, as a vascular bundle was found in the vicinity of the surface which failed to cicatrize (fig. 4).

The foregoing observations indicate the diversity of wound reaction in very limited areas. From these results the writer is inclined to believe that more detailed studies of other species will reveal similar unreported wound responses.

The writer wishes to express appreciation to Professor H. H. York for his interest and assistance in this investigation.

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INDEX TO AMERICAN BOTANICAL LITERATURE

1931-1936

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Pollen grains in the identification and classification of plants. VII. The Ranunculaceae

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(WITH PLATE 20 AND ONE TEXT-FIGURE)

The pollen grains of the Ranunculaceae comprise several forms of widely different aspect. For the most part these are obviously related to each other, but they show that several divergent trends of development are well established. A correct understanding of these forms is of the utmost importance on account of the key position assigned to the Ranunculaceae among the dicotyledons.

The basic form, the form which characterizes the pollen grains of more than half of the species studied, is typified by the grains of *Ranunculus* (fig. 7). It is provided with a fairly thin, flexible, but not distensible exine. The relatively huge changes in volume to which pollen grains are always subjected with changing moisture content are accommodated by three long meridonally arranged furrows, called germinal furrows because they also permit the emergence of the pollen tube at time of germination. Each is crossed by a delicate elastic membrane which is nearly always flecked with fragments of material closely resembling that of the exine. When the grains are moist and fully expanded these flecks stand apart from each other, exposing much of the stretched membrane, but when the grains are even moderately dry and partly contracted the flecks are pressed closely together and against the margins of the furrow so that the grain is protected by what amounts to a continuous covering of exine throughout its entire surface. These furrows are further characterized by the total absence of germ pores—the whole furrow area serving as a place of emergence for the pollen tube—and by lack of thickened furrow rims, in these respects differing from perhaps the majority of three-furrowed grains of other families. The furrow margins are most commonly poorly defined, the texture of the general surface of the exine merging into the flecked surface of the furrow membrane, the two sometimes not even distinguishable from each other, unless the grains are expanded when the furrows are revealed by the separation of the flecks on their membranes as they stretch. The furrow margins are generally rough, jagged, or even fimbriate, sending long processes of exine-like material out onto the furrow membrane. These characters of the furrows, while undergoing some modifications within the family, are peculiar to the Ranunculaceae and, to a lesser extent, some of the more primitive monocotyledons, and are of profound phylogenetic significance.

[THE BULLETIN FOR NOVEMBER (63: 429-494) WAS ISSUED NOVEMBER 2, 1936]

The mechanism whereby the furrows permit changes in volume without rupturing the exine is rather complex, but may be resolved into three more or less distinct movements. When a grain such as that of *Caltha*, for example, is quite dry and of its minimum volume, it is of an elongate form, perhaps twice as long as broad (fig. 10), and provided with three deep longitudinal grooves so that in section it appears deeply three lobed. With the expansion due to taking up moisture the first movement is the pushing out of the grooves until the grain becomes ellipsoidal and more nearly circular in outline, the furrows up to this stage remaining unexpanded and merely acting as hinges. In some grains in which the furrows are demobilized by heavy encrustations of exine material on their membranes the *hinge action* is the only movement permitted them, such grains remaining elongate even when fully expanded, for example those of *Adonis* (fig. 9). More often, however, as the turgidity of the grain increases the furrows expand, stretching their elastic membranes and becoming spindle shaped, the grain at the same time becoming shorter and broader until it is almost spherical or even oblately flattened, but still circular in section (fig. 4). This *furrow expansion* appears to be the most effective movement in the adjustment of volume, for, by changing its shape from ellipsoidal to spheroidal, the volume of the grain is greatly increased with a small amount of stretching of its furrow membranes and without materially increasing its surface. The majority of grains appear to require no further increase in volume than is permitted by the mechanism of furrow expansion. Further increase in volume, however, may be achieved by an outward distension of the furrow membranes forming a sort of aneurysm at each of the furrows, if I may be permitted to borrow a medical term which is used to describe the sudden distension of an artery wall to the limit of its elasticity under the influence of either excessive pressure from within the artery or a loss of tension of its wall. *Membrane distension* of this kind in pollen grains is generally accompanied by a flattening of the walls of the grain in the equatorial region, especially if the exine is thin, the grain assuming a rounded-triangular outline (fig. 1).

Among the tricolpate grains of the Ranunculaceae generally all three of these movements are more or less involved, but in the pollen of the majority of species furrow expansion is the favored movement, hinge action and membrane distension playing relatively minor rôles. Hence it is that the furrows of the grains described in the following pages are generally long and tapering to narrowed or pointed ends (fig. 7), for this kind of furrow is best adapted to the expansion movement. Those in which the hinge action is paramount are long and narrow, and not generally tapering much (fig. 9). And those in which membrane distension is

the major function are broad, generally rather short, and with broad rounded ends (fig. 2). It is in these furrow characters that differences between the different species are mainly expressed, especially among those which are closely related. Their phylogenetic significance is not deep seated, closely related species often showing rather extreme differences in these respects.

The characters of the exine show much less variation and appear to be phylogenetically much more deep seated than those of the mechanical action of the furrows. In its basic form the exine is rather thin—thin enough to be freely flexible, but thick enough to be indistensible—more or less granular and covered with minute papillae which are irregular in arrangement and various in size. In the grains of some species papillae are strongly developed, almost reaching the size of spines; in others they are vestigial or even entirely absent, this condition being generally associated with correspondingly more pronounced granulation of the exine. Occasionally the papillae appear to coalesce forming a rudimentary reticulum (e.g. *Nigella*). For the most part the different species exhibit only different degrees in the relative development of the granular and papillate characters, but there are two other types of exine found within the family which have no obvious connection with these. One is the striate, found only in the three species of *Trollius* and the other is the pitted or reticulate, found in the grains of *Helleborus*, *Hydrastis* and *Paeonia* (fig. 1). The striate form can, perhaps, be interpreted as a derivative of the ordinary granular form in which the granules are arranged in rows; and possibly the reticulate form can be regarded as representing the coalescence of the papillae already initiated in the grains of *Nigella*. This latter, however, is uncertain because the reticulum of all the truly reticulate grains is much finer than that adumbrated in the grains of *Nigella*.

The basic form of grain of the Ranunculaceae may, therefore, be described as: approximately spheroidal, tricolpate; furrows long, broad and tapering to narrowed ends, their membranes flecked, their margins rough, jagged, or fimbriate; exine rather thin, more or less granular and papillate; in size various from about 20–30 μ in diameter. Such a form is illustrated by the grain of *Ranunculus* (fig. 7), and characterizes, without serious modification those of about 20 of the 29 genera examined in this study (see key, p. 500).

The most important modifications of this basic form have to do with the furrows. The flecks on the furrow membrane, copious but discrete and irregular in arrangement in the basic form, are reduced in number or entirely absent in the grains of *Paeonia* (fig. 1). In others they are aggregated in various ways forming irregular patches or strips of exine-like

material on the furrow membrane, often fused to the furrow margins forming fimbriae, as in the grains of *Eranthus*, or aggregated in a central strip, as in those of *Hepatica*. The culmination of this developmental tendency seems to be reached in the grains of *Adonis aestivalis* (fig. 9), in which the furrow membrane is heavily encrusted with a central strip of exine material, and the furrows partly demobilized, deprived of nearly all movement except their hinge action.

Another modification is the substitution of rounded or irregularly shaped pores for the furrows in such grains as those of *Coptis*, *Syndesmon* and *Thalictrum* (figs. 3, 5, 8). The pores of these grains have all the other more important characteristics of the furrows of their closest relatives, such as their flecked membranes and their rough, jagged or fimbriate margins. In their number and arrangement, however, they do not always conform to the trischistoclastic system which governs the arrangement of the furrows, and in their harmomegathic function they possess only that of membrane distention, compensating for the lack of hinge action and furrow expansion by their larger number.

The pored form appears to have originated in this family more than once independently and at widely different times. It occurs in the anemophilous genus *Thalictrum*. Whether or not in this case there is any relation between anemophily and the pored condition can not be said, though the occurrence in this genus of both conditions which are exceptional in the family, suggests that there may be. The pored condition occurs in the Malayan genus *Naravelia*. These are woody climbers distinguished by the possession of connate carpels, divergent in this and in their southward distribution from the central ranalean type. In these two cases, at least, the pored character belongs to divergent groups, suggesting that it may be of recent origin. The same character, however, occurs in the grains of *Coptis trifolia* and *Xanthorrhiza apiifolia*. Both are North American plants, the former a herb of northern latitudes, occurring as far north as British Columbia and Alaska, the latter a shrub of more southern latitudes, from southern New York to Kentucky and Florida. The plants have so many things in common—their yellow roots, their bitter taste, their shining leaves which are trifoliate when basal—besides the practical identity in form of their pollen grains, that there can be little doubt that they are closely related. Possibly *Coptis* may be regarded as a northern herbaceous off-shoot from some ancestral stock of which *Xanthorrhiza* is a conservative survivor of more temperate regions. It would, therefore seem that, in this case at least, the pored character of the pollen grain is more ancient than the herbaceous habit. The same character is found in the grains of *Anemone coronaria* but is absent from the five other species

of *Anemone* which I have examined. These four rather widely separated occurrences suggest that this character has originated among the Ranunculaceae more than once. It is perhaps to be regarded as only a tendency in this family, and we may expect to find it more fully expressed in some of the derivatives of the Ranalean complex.

The ways in which pores have been derived from furrows is not entirely clear because most of the intermediate forms are lacking. Nevertheless, some of both the pored and furrowed grains of this family possess peculiar characteristics which are suggestive of how this might have come about. Among the pored grains the arrangement of the pores occasionally tends to conform to the trischistoclastic system as if the pores represented shortened furrows. In the grains of *Coptis* (fig. 3) and of *Xanthorrhiza*, for example, the pores are commonly arranged in triangular groups of three which suggest the triconvergent grouping of furrows arranged in this system. And in the grains of *Thalictrum dioicum* (fig. 8) the prevailing number of pores on the whole grain is six arranged exactly tetrahedrally, corresponding to the hexacolpate configuration of furrows. Such regularity of arrangement, however, is not the general rule. More typical is the condition found in the grains of *Syndesmon* (fig. 5). In these the pores are irregular in their size, shape and arrangement, they never suggest any complete furrow configuration, and frequently some are elongate, sometimes almost long enough to be regarded as furrows. Generally such elongate pores are curved or 'v' shaped and suggest that they may represent fragments of zonate and zigzag furrows. This is significant because among those grains of the family which have supernumerary furrows the ordinary furrow configurations are not usually found completely developed. The pollen of *Batrachium* is such an example. Here the grains all possess supernumerary furrows but instead of the usual symmetrical arrangements, the zonate, half zonate and zigzag arrangements are the most frequent. This is likewise true of the grains of *Ranunculus acris*. The furrows of these are also short and broadly rounded so that in many cases they have a striking resemblance to the elongate pores of the grains of *Syndesmon*. It would therefore seem that sometimes, as in the grains of *Coptis* and *Thalictrum*, the pores represent shortened furrows arranged in the trischistoclastic system, but in others, as in the grains of *Syndesmon* and *Anemone*, the pores represent fragments of furrows.

PAEONIA ALBIFLORA Pallas. Peony (fig. 1). Grains various, a large proportion of them obviously abortive. Normal grains oblate and triangular in outline when fully expanded, about 34μ in diameter, tricolpate. Furrows long, broad, and tapering to rounded ends, their membranes smooth or faintly flecked, their margins jagged but sharply defined. Exine moder-

KEY TO THE SPECIES

- A. Exine granular, papillate, or both (papillae tending to fuse to form a reticulum in *Nigella*).
1. Furrows elongate, generally three meridionally arranged, though some grains of most species (all in *Pulsatilla alpina* and *Batrachium sp.*) may have higher numbers arranged irregularly or in the trischistoclastic system, their membranes more or less flecked.
 - i. Exine distinctly papillate and more or less granular.
 - a) Furrow ends broad and rounded.
 - 1) Furrow margins smooth, and furrows broad, scarcely tapering. *Caltha*
Anemone demissa
 - 2) Furrow margins rough or jagged, and furrows tapering.
 - Grains more than $25\ \mu$ in diameter. *Ranunculus*
 - Grains small, about $19\ \mu$ in diameter. *Isopyrum*
 - b) Furrow ends pointed. *Pulsatilla*
Hepatica
Eranthis
 - c) Furrow ends irregular and margins jagged. *Actaea*
Cimicifuga
Anemone Davidi
quinquifolia
virginiana
Clematis
Myosurus
Oxygraphis
Trautvetteria
Batrachium
Nigella
Glaucidium
 - ii. Exine granular, scarcely or not at all papillate. Furrow ends pointed or somewhat blunt.
 - a) Furrows broad and tapering to pointed ends. Exine not excessively thick.
 - Grains slightly umbonate, $21-29\ \mu$ in diameter. *Aconitum*
Delphinium
 - Grains not umbonate. *Aquilegia*
 - b) Furrows narrow, partially demobilized by a heavy encrustation on their membranes
 - Exine excessively thick. Grains $25-27.5\ \mu$ in diameter.
 - Grains conspicuously umbonate. Exine only granular. *Adonis aestivalis*
 - Grains not umbonate. Exine granular and faintly papillate. *Adonis vernalis*
 2. Furrows, in the ordinary sense, absent, their function being served by a number of rounded or irregularly shaped pores.
 - i. Exine distinctly papillate.
 - a) Grains small $16-18.5\ \mu$ in diameter.
 - Pores about 10, various. *Coptis*
 - Pores 15 or more, circular. *Xanthorrhiza*
 - b) Grains larger, over $22\ \mu$ in diameter.
 - Pores uniformly circular. *Anemone coronaria*
 - Pores circular to elongate. *Syndesmon*
 - ii. Exine granular, occasionally slightly papillate. *Naravelia*
Thalictrum
- B. Exine reticulate-pitted or frankly reticulate, furrows generally three meridionally arranged.
1. Furrow margins smooth. *Helleborus*
 2. Furrow margins rough.
 - i. Furrow membranes copiously flecked. *Hydrastis*
 - ii. Furrow membranes nearly or quite smooth. *Paconia*
- C. Exine striate, furrows generally three, their membranes flecked. *Trollius*

ately thick, reticulate pitted. Intine thin, slightly thickened in the region underlying the furrow.

In the reticulate character of their exine these grains resemble those of *Helleborus* and *Hydrastis* but are otherwise unique in the family.

A garden perennial, native of Siberia, China and Japan.

GLAUCIDIUM PALMATUM S. & Z. Grains uniform, spheroidal, about 25.5μ in diameter, tricolpate. Furrows long and tapering to blunt ends, not excessively broad when expanded, their membranes conspicuously flecked and their margins jagged to almost fimbriate. Exine thin, papillate granular.

These grains conform in all respects with the basic form of the family but are dissimilar to those of *Paeonia* with which genus *Glaucidium* is associated in the tribe Paeonieae according to Engler.

The genus comprises only this species, native of Japan.

HYDRASTIS CANADENSIS L. Yellow root, yellow puccoon, golden seal. Grains uniform, spheroidal, $21-25.5\mu$ in diameter, tricolpate. Furrows long and tapering, their membranes conspicuously flecked, their margins rough. Exine finely reticulate.

These grains resemble those of *Helleborus* in most respects. In their reticulate character, which is unusual in this family, they also resemble those of *Paeonia* with which they are associated in the tribe Paeonieae.

A low herbaceous perennial arising from a bright yellow rootstock. Native of the eastern United States and Canada.

CALTHA L. Marsh marigold

Grains uniform oblate and somewhat triangular in outline when expanded, $25-35\mu$ in diameter, tricolpate. Furrows long and broad, scarcely tapering to broad rounded ends, their membranes more or less thickly covered with flecks, their margins smooth. Exine moderately thick, granular, and densely coated with minute papillae similar to the granules of the furrow membranes.

These grains differ from the type of the family only in the less papillate surface of the exine and broader furrows with smoother margins.

The genus comprises about 15 species of low marsh or semiaquatic herbs with large undivided leaves, generally cordate or reniform, distributed throughout the temperate and arctic regions of both hemispheres.

CALTHA PALUSTRIS L. Marsh marigold (fig. 2). Grains about 25μ in diameter. Furrow margins nearly or quite smooth, their membranes lightly flecked.

Native of northeastern United States and Canada.

CALTHA RADICANS Forst. Grains similar to those of *C. palustris*, their

furrow membranes more conspicuously flecked, their margins smooth but almost obscured by the granules of the furrow membranes.

The plant is similar to the above but roots from the lower nodes and has smaller flowers.

TROLLIUS L. Globeflower

Grains spheroidal or somewhat ellipsoidal, circular or three-lobed in outline, 17–26 μ in diameter, tricolpate, occasionally some with aberrant numbers of furrows. Furrows long and tapering to irregularly shaped or rounded ends, their membranes flecked with granules, their margins smooth, granular, or even fimbriate. Exine thick and striate with the striae arranged in patterns resembling thumb-prints.

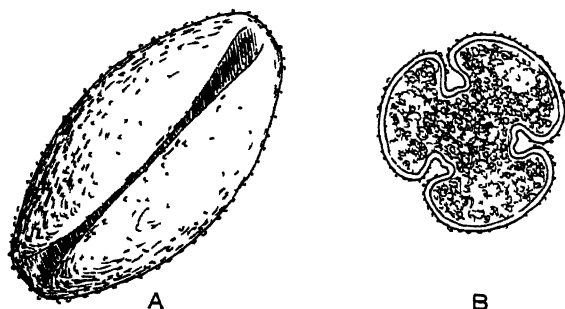


Fig. 10. *Caltha palustris*. A. Side view. B. transverse optical section.

The striate character of these grains has not been found elsewhere in this family, but similar markings are found on the grains of most Aceraceae and Rosaceae.

The genus comprises about 12 species of erect perennial ascending herbs resembling *Caltha*, mainly inhabiting marshy places. Native of the north temperate Zone.

TROLLIUS ALBIFLORUS (Gray) Rydbg. Grains uniform, spheroidal, about 25 μ in diameter. Furrow margins fimbriate. Exine thick and rigid, thumb-print markings pronounced.

Herbaceous perennial of mountain tops, Colorado, and northward and westward.

TROLLIUS EUROPAEUS L. Globeflower. Grains ellipsoidal, three lobed in outline, tricolpate, 17–18 \times 20–22 μ . Furrow margins rough but not quite fimbriate. Otherwise as in *T. albiflorus*.

Herbaceous perennial of wet uplands, northern Europe.

TROLLIUS LEDEBOURII Reichb. f. A large proportion of the grains small and apparently abortive. Normal grains 19–21 μ in diameter,

spheroidal. Furrows long, broad and tapering to rounded ends, their margins smooth. Exine rather thick but less so than in *T. albiflorus* and the striate markings less conspicuous.

Herbaceous perennial occasionally found in cultivation, native of Siberia.

HELLEBORUS Tourn. Hellebore

Grains uniform excepting a few that are abortive, oblately flattened and triangular in outline when expanded, about 30μ in diameter, tricolpate. Furrows very broad and long, tapering to narrow but rounded ends, their membranes conspicuously flecked with rounded granules irregularly arranged, their margins smooth. Exine thin, finely and uniformly reticulate throughout, the reticulum ending with closed lacunae along the furrow margins.

These grains deviate rather widely from the type in the reticulate nature of their exine and the smooth margins of their furrows.

The genus comprises 15 perennial herbs with palmate leaves and large solitary nodding flowers appearing in early spring. Native of Europe and western Asia, some species introduced into North America, both wild and cultivated.

HELLEBORUS FOETIDUS L. Hellebore. Grains about 27.4μ in diameter. The ridges of the reticulum confluent along the margins of the furrows forming a thickened rim.

Native of northern Europe, cultivated elsewhere.

HELLEBORUS VIRIDIS L. Green hellebore. Grains as in *H. foetidus*

Native of Europe and Asia.

ERANTHIS LONGISTIPITATA Rgl. Winter aconite. Grains spheroidal or slightly oblately flattened, tricolpate. Furrows long, broad and tapering to narrowed but irregularly shaped ends, their membranes copiously flecked with large and coalescent granules, their margins jagged or fimbriate. Exine rather thick, papillate. Intine thick.

In these grains we see a most extreme manifestation of the tendency, characteristic of the family, for the furrow membranes to become obscured by granules of exine-like material. The granules resemble the papillae of the exine, they are large and coalescent with each other and with the jagged marginal projections forming fimbriae which reach almost entirely across the furrow.

The genus comprises about 7 species of perennial herbs with palmately multifid leaves from which arise one-flowered scapes surrounded by an involucre of a single leaf. Native of Europe, eastern and central Asia. *E. hyemalis* Salisb. sparingly naturalized in North America.

NIGELLA INTEGRIFOLIA Rgl. Fennel flower. Grains various, a large proportion abortive, normal grains oblately flattened, triangular in outline, $31-41\mu$ in diameter, tricolpate. Furrows of medium length, broad and tapering to narrow but irregularly-shaped ends, their membranes flecked with granules similar to the papillae of the exine, their margins jagged and somewhat fragmenting. Exine thin, papillate with the papillae fusing to form an imperfect reticulum. Intine thick but not noticeably thicker in the regions of the furrows.

The papillae of the exine of these grains are similar to those of the furrow membranes, but in the latter situation they are more widely separated and appear to be sharply raised above the surface while on the exine they are less raised and more closely aggregated.

The genus comprises about 16 species, native of Europe.

ISOPYRUM L. Shell flower

Grains ellipsoidal to spheroidal, $18-19\mu$ in diameter, tricolpate. Furrows long, broad and tapering, their membranes flecked, their margins rough. Exine rather thick, papillate.

Slender smooth perennial herbs with compound leaves and axillary white flowers resembling those of *Syndesmon*. The genus comprises about 30 species native of North America, Asia and Japan.

ISOPYRUM FUMARIOIDES L. Grains as in generic description, about 19.4μ in diameter.

Native of Europe and northern Asia.

ISOPYRUM HENRYI Oliv. Grains as in the generic description, about 18.7μ in diameter.

Native of China.

COPTIS TRIFOLIA Salisb. Three-leaved goldthread (fig. 3). Grains spheroidal, $17-18.5\mu$ in diameter. Pores about 10, their membranes flecked with conspicuous granules, generally prominently bulging, their margins fimbriate, various in size and shape but generally nearly circular. Exine rather thick, papillate.

These grains are similar to those of *Xanthorrhiza*, *Anemone coronaria*, *Syndesmon*, *Naravelia* and *Thalictrum* within the family, but may be distinguished by the more fimbriate margins of their pores. Outside of the family they closely resemble the grains of the Alismaceae and some Butomaceae but may be distinguished from these by the character of their exine which is papillate while in these two latter families it is more nearly echinate.

The three-leaved goldthread is a low perennial herb with ternately divided root leaves, small white flowers on slender scapes, and roots of

long bright yellow fibers. Native of north eastern United States and Europe. The genus comprises about 8 species, principally of North America.

XANTHORRHIZA APIIFOLIA L'Her. (*X. simplicissima* Marsh.) Shrub yellowroot. Grains similar to those of *Coptis*, uniform. 16–18.5 μ in diameter. Pores about 15, somewhat smaller than in the grains of *Coptis*, and their margins less conspicuously fimbriate.

A low shrubby plant with bark and roots deep yellow. Native of eastern United States from Pennsylvania southward.

A small genus of shrubby plants native of eastern North America cultivated for their foliage. The name is frequently written, *Zanithoriza*, an older form though etymologically incorrect.

ACTAEA SPICATA L. Baneberry. Grains uniform, oblate-spheroidal, 27–31 μ in diameter, tricolpate. Furrows long, broad and tapering, their membranes conspicuously flecked, their margins ragged almost fimbriate. Exine rather thick, papillate.

A perennial herb in woods, northeastern United States and Canada. The genus comprises about 6 species native of the north temperate Zone.

CIMICIFUGA L. Black Cohosh, bugbane

Grains oblate spheroidal, 23–26 μ in diameter, tricolpate. Furrows medium long, tapering to irregularly shaped ends; their membranes conspicuously flecked, their margins jagged, almost fimbriate. Exine thick and firm, granular, papillate and marked with angular areas enclosing the papillae. Intine thick and further thickened in the regions underlying the furrows.

The genus comprises eleven species of tall perennial herbs bearing long spikes of white flowers with the stamens exserted suggesting that they may be partly anemophilous, closely related to *Actaea*, widely distributed in the north temperate zone.

CIMICIFUGA DAHURICA Huth. Grains as in the generic description. Native of central Asia.

CIMICIFUGA FOETIDA L. Grains as in the generic description. Native of Europe and Asia.

AQUILEGIA L. Columbine

Grains spheroidal or slightly oblately flattened, rounded-triangular in outline, 21–29 μ in diameter; tricolpate, generally some with supernumerary furrows. Furrows long, broad and tapering to pointed ends, their membranes conspicuously flecked, their margins differing in the different species from smooth to jagged or even somewhat fimbriate. Exine more or less

granular and minutely papillate, mostly thin but various in the different species. Intine thin and not visibly thickened in the regions of the furrows.

About 50 species of erect branching perennial herbs with compound leaves and large showy flowers, widely distributed throughout the north temperate zone.

AQUILEGIA CANADENSIS L. Wild columbine (type). Grains somewhat various; some obviously abortive, others with supernumerary furrows. Furrow membranes conspicuously flecked with granules irregularly arranged, furrow margins jagged or even somewhat fimbriate owing to the coalescence of some of the granules of the membrane with the jagged projection of the margins. Exine thin, faintly granular and finely papillate.

Perennial herbs in dry rocky woods almost throughout the eastern half of the United States and Canada.

AQUILEGIA VULGARIS L. Garden columbine. Grains mostly uniform, about 22μ in diameter, generally a small proportion tetra- and hexacolpate. Furrow membranes less conspicuously flecked than in the type.

Native of Europe and Siberia, widely cultivated in several varieties, and occasionally escaped in the United States.

AQUILEGIA GLANDULOSA Fisch. Grains uniform, about 21.6μ in diameter, tricolpate. Furrow membranes flecked with large and conspicuous granules, furrow margins rough. Exine thicker than in the type, slightly more granular, scarcely papillate.

Native of the Altai mountains, Siberia, but widely cultivated in the United States and elsewhere.

AQUILEGIA FLABELLATA S. & Z. Grains uniform, $25-29\mu$ in diameter. Furrow membranes flecked with large conspicuous granules which tend to be arranged in rows, otherwise as in *A. glandulosa*.

Native of Japan but widely cultivated elsewhere.

DELPHINIUM L. Larkspur

Grains generally uniform, $25-29\mu$ in diameter, spheroidal, ellipsoidal or slightly oblate, tricolpate, generally with a slight elongate mound due to the arching up of the exine, extending meridionally in each lune. Furrows, long, broad and tapering, their membranes conspicuously flecked with granules which tend to aggregate or coalesce into irregular groups, their margins roughened, jagged or fimbriate. Exine rather thin but somewhat thickened at the poles causing the grains to be slightly umbonate, finely but conspicuously granular.

These grains closely resemble those of *Aquilegia* but may be distinguished by their larger size, generally elongate and umbonate form.

The genus comprises about 250 species of perennial and annual erect herbs with showy flowers, in north temperate regions.

DELPHINIUM CAERLEUM Jacq. Grains spheroidal, ellipsoidal or slightly oblately flattened, about 28.5μ in diameter. Furrow margins roughened to fimbriate.

Native of Himalaya.

DELPHINIUM BULLEYANUM G. Forr. Grains spheroidal to ellipsoidal, about 27μ in diameter. Furrow margins jagged.

Native of China.

DELPHINIUM BONATII Léveillé. Grains ellipsoidal, about $25 \times 27\mu$. Furrow margins fimbriate.

Native of China.

ACONITUM L. Aconite, monkshood

Grains spheroidal, ellipsoidal, or more or less oblate, $21-27\mu$ in diameter, tricolpate. Furrows long broad and tapering to irregularly shaped ends, their membranes copiously flecked with large granules, their margins jagged. Exine thin, finely granular.

These grains bear a close resemblance of those of *Delphinium* in the characters of their furrows and their exine, and two of the species here described are likewise umbonate.

Perennial herbs with palmately cleft or dissected leaves and showy flowers in racemes or panicles, closely resembling *Delphinium*. About 70 species in the higher parts of the north temperate zone.

ACONITUM DELPHINIFOLIUM DC. (fig. 4). Grains uniform, slightly oblately flattened, triangular in outline, $23-26\mu$ in diameter, not umbonate.

Moist places, Alaska to Alberta to British Columbia.

ACONITUM DIVARICATUM Rydb. Grains spheroidal, scarcely three-lobed, $25-26\mu$ in diameter. Otherwise as in *A. delphinifolium*.

Creek banks. Idaho to Utah to Wyoming.

ACONITUM HELLERI Greene. Grains spheroidal, ellipsoidal or slightly oblately flattened, $21.5-23\mu$ in diameter, umbonate as in those of *Delphinium*.

Native of North America.

ACONITUM COLUMBIANUM Nutt. Western monkshood. Grains somewhat various, generally a large proportion abortive. Normal grains nearly spheroidal, $23-27.5\mu$ in diameter, similar to those of *A. Helli* but less umbonate.

Wet meadows and borders of streams, California and Arizona.

ANEMONE L. Anemone

Grains of two types, those with furrows and those with pores (*A. coronaria*). Grains with furrows oblately flattened, $20-28\mu$ in diameter,

circular or somewhat triangular in outline, tricolpate. Furrows long, more or less tapering to broad rounded or jagged ends, their membranes conspicuously flecked with granules which resemble the papillae of the exine, their margins slightly roughened, jagged or fimbriate. Exine always conspicuously papillate, occasionally marked off into angular areas containing the papillae. These grains are similar to those of *Delphinium* but may be distinguished by their smaller size, flattened form and papillate exine.

The pored grains are similar to those of *Coptis* but may be distinguished from them by their larger size. Though these pored grains present a very different appearance from the furrowed grains of this genus, in reality they differ only in the number of their furrows, since the pores are morphologically merely reduced furrows; in all other respects they are the same as the furrowed grains of *Anemone*.

ANEMONE JAPONICA S. & Z. Japanese anemone. A large proportion of the grains abortive and variously irregular in shape. Normal grains oblate, rounded triangular in outline, 20.5μ in diameter. Furrows long, broad, and tapering to irregularly shaped ends, their membranes conspicuously flecked with rounded granules variously aggregated.

A stout branching plant with soft hairy basal leaves. Native of China and Japan, extensively cultivated elsewhere.

ANEMONE DEMISSA Hook. f. Grains similar to those of *A. japonica*, about 26μ in diameter. Furrows long, broad and tapering to symmetrically rounded ends, their membranes flecked with granules which may be separately dispersed or more or less arranged in striae, their margins nearly smooth, slightly roughened by the attachment to them of a few granules.

Himalaya.

ANEMONE DAVIDI Fr. Grains about 27.4μ in diameter. Furrows long and narrow, not greatly expanded at the center, their membranes flecked with scattered granules, their margins jagged.

These grains can be distinguished from those of the two preceding species by their narrower furrows with more jagged margins. In other respects they are similar.

Native of China.

ANEMONE VIRGINIANA L. Tall anemone. Grains $22.5\text{--}24\mu$ in diameter. Furrow membranes flecked with granules which tend to coalesce in a central strip. Otherwise as in those of *A. Davidi*.

Common in woods in the eastern United States.

ANEMONE QUINQUEFOLIA L. Wind-flower, snow drops. Furrow membranes flecked with scattered granules, furrow margins jagged. Otherwise as in the grains of *A. virginiana*.

Native of eastern United States and Canada, closely resembling *A. nemorosa* which is native of Europe but cultivated in the United States.

ANEMONE CORONARIA L. Poppy anemone. Grains somewhat various, a large proportion obviously abortive, $22-32\mu$ in diameter, spheroidal with about 15-18 pores which are variously irregular, sometimes elongate, but generally approximately circular, their membranes heavily flecked with granules which tend to be aggregated towards the center, their margins rough. Exine rather thick and papillate as in other species of anemone.

The poppy anemone is native of the Mediterranean region, now a favorite hot-house plant cultivated in many varieties. The one from which the present specimen of pollen was obtained is known as "Craig Castle Improved."

PULSATILLA Adans. Pasque flower

Grains essentially as in *Anemone japonica*, $29-36\mu$ in diameter, tricolpate or with supernumerary furrows. Furrow margins rough but not fimbriate. Exine rather thick, granular, and papillate.

The genus comprises about 18 species of perennial scapose herbs with thick root stocks, native of the north temperate and subarctic zones. In many classifications (e.g. Engler and Prantl) the group is regarded as a section of the genus *Anemone* to which it is undoubtedly closely related.

PULSATILLA HACKELII Pohl. Grains uniform $34-37\mu$ in diameter, tricolpate.

PULSATILLA LUDOVICIANA Heller (*P. hirsutissima* Britt.). Grains various. $37.5-44.5\mu$ in diameter, a large proportion with supernumerary furrows.

Plains and prairies. Almost throughout the United States and Canada west of Illinois.

PULSATILLA ALPINA Schrank. Grains extremely various, $29-33.5\mu$ in diameter. Furrows generally more than three, a large proportion of the grains with 6, 12, and 15 furrows arranged according to the trischistoclastic system, others with furrows irregularly arranged.

SYNDESMON THALICTROIDES Hoffmg. (*Anemonella thalictroides* Spach.) Rue-anemone (fig. 5). Grains exceedingly various, $15-45\mu$ in diameter. Furrows absent. Pores about 12-15, in the smaller grains circular, in the larger circular or variously irregular, their margins rough or jagged, more so in the larger grains. Exine rather thick, granular and papillate.

Normal grains of this pollen are of two sizes, exclusive of those which are obviously abortive. The larger are about 40μ in diameter while the smaller are about 20μ in diameter. The exine appears the same in both; it is of the same thickness, of the same granular nature and the papillae

which almost reach the proportions of spines, are of the same size. The result, however, is that the smaller grains appear to have a very thick and coarse exine. The number of pores in each bears no relation to the size of the grain; the smaller grains have the smaller pores so that the proportion of the surface occupied by pores is about the same in each. In the smaller grains, however, the pores are always approximately circular, while in the larger they may be elongate, even resembling ordinary furrows.

The genus comprises only this species, a low glabrous perennial herb, 4-9 inches high, resembling *Anemone quinquefolia*, with which it is often associated in woods throughout the eastern United States.

HEPATIC TRILOBA Chaix. Liver-leaf. Grains somewhat various, 28-30 μ in diameter, oblate spheroidal, tricolpate. Furrows long narrow and tapering to jagged ends, their membranes rather thick and copiously flecked with papillae which tend to be aggregated in a band in the center of the furrow like a central strip of exine. Furrow margins rough or jagged, often with adhering flecks of the furrow membrane.

Native of eastern United States and Canada, also in Europe, Alaska and Asia.

CLEMATIS L. Clematis

Grains oblately flattened and rounded triangular in outline or spheroidal, 19-25.5 μ in diameter, tricolpate, occasionally otherwise. Furrows long and tapering, their membranes more or less copiously flecked with coarse granules variously aggregated, their margins smooth or jagged, generally with strands or clusters of the membrane granules adhering. Exine rather thick, conspicuously papillate. Intine thick and further thickened beneath the furrows.

Climbing vines more or less woody, with cymose paniculate flowers. About 25 species of cosmopolitan distribution.

CLEMATIS MONTANA Buch.-Ham. (fig. 6). Grains various, a large proportion abortive. Normal grains oblate, rounded triangular in outline, 19-25.5 μ in diameter. Furrows long and tapering to rounded ends, their membranes only sparsely flecked.

A tall climber, reaching 15-20 ft. Native of Himalaya, cultivated elsewhere.

CLEMATIS PICKERINGII Gray. Grains spheroidal, about 22.8 μ in diameter. Furrow membranes densely covered with papillae rendering them scarcely distinguishable from the exine. Otherwise as in *C. montana*.

NARAVELIA ZEYLANICA DC. Grains uniform, 17-19 μ in diameter. Furrows absent. Pores about 15, approximately circular, their membranes

thick and densely flecked with granules rendering them similar in appearance to the exine. Exine rather thick, finely but conspicuously granular.

These grains resemble those of *Coptis* and *Syneddesmon* but may be distinguished by their granular instead of papillate exine. They also resemble those of *Thalictrum* but may be distinguished by their smaller size. In their tendency towards obliteration of the pores they resemble those of some species of *Alisma*.

Perennial climber, native of Malaya.

MYOSURUS MINIMUS L. Mouse-tail. Grains uniform, spheroidal, about 20μ in diameter, tricolpate. Furrows long broad and tapering to jagged ends, their membranes flecked with granules resembling the papillae of the exine, their margins jagged. Exine rather thin, papillate. Intine thin but thickened beneath the furrows.

A low annual with linear-spatulate leaves and naked one-flowered scapes. Native of the central and southern parts of the United States, and Europe. The genus contains about 5 species principally of North America.

TRAUTVETTERIA GRANDIS Nutt. False bugbane. Grains uniform, about 25μ in diameter, tricolpate, occasionally some grains otherwise. Furrows long and narrow, scarcely tapering to irregularly shaped ends, their membranes copiously flecked and margins fimbriate, both to such an extent that the furrows are nearly obliterated. Exine rather thick, papillate, faintly marked off into angular areas enclosing the papillae.

A perennial herb with palmately lobed leaves and corymbose white flowers, resembling *Cimicifuga*, apparently partly adapted to wind pollination. British Columbia to California and eastward to Montana; eastern Asia. The genus comprises only this species.

OXYGRAPHIS CYMBALARIA Prantl (*Ranunculus Cymbalaria* Pursh, *Halerpestes Cymbalaria* Greene). Seaside crowfoot. Grains spheroidal, $19-20.5\mu$ in diameter, tricolpate. Furrows long and tapering, their membranes heavily flecked, their margins not sharply defined, the texture of the furrow membranes merging with that of the general exine. Exine papillate. Intine thin.

Low glabrous herb with mostly basal cordate leaves, spreading by runners. On sandy shores, northeastern United States and Canada. The genus comprises about 9 species in central and eastern Asia, and North America, frequently regarded as a section of the genus *Ranunculus*.

RANUNCULUS Tourn. Crowfoot, buttercup

Grains spheroidal or oblatelly flattened, about $22-32\mu$ in diameter, tricolpate, occasional grains tetra- and hexacolpate or variously irregular. Furrows long and tapering to broadly rounded ends, their membranes

flecked with conspicuous granules, their margins jagged or fimbriate. Exine thin, papillate.

The genus comprises more than 200 species of low terrestrial or aquatic herbs of wide distribution.

RANUNCULUS ABORTIVUS L. Small-flowered buttercup (fig. 7). Grains mostly normal $22.5\text{--}26.5\mu$ in diameter.

Woods and moist places almost throughout the United States and Canada east of the Rocky Mountains.

RANUNCULUS ACRIS L. Tall crowfoot, buttercup. Grains mostly with supernumerary furrows, short with rounded ends, their membranes copiously flecked, $26\text{--}32\mu$ in diameter.

Almost throughout Europe and North America.

RANUNCULUS PURSHII Richards. Grains similar to those of *R. abortivus*, about 30μ in diameter.

A glabrous aquatic herb with filiformly dissected leaves, wholly immersed or creeping on muddy banks. Throughout northern United States and Canada.

BATRACHIUM Water crowfoot

Grains essentially as in *Ranunculus*, tricolpate or with six or more furrows, the latter broad and tapering to rounded or jagged ends, their membranes conspicuously flecked. Exine thin papillate. Intine thin and not thickened beneath the furrows.

Aquatic perennials with immersed dissected leaves and aerial flowers. Closely related to *Ranunculus*.

BATRACHIUM CONFERVOIDES Fries. (*Ranunculus aquatilis* L.). Grains uniform, about 27μ in diameter, tricolpate.

Common, especially in slow-flowing streams almost throughout the United States and Canada.

BATRACHIUM sp. Grains uniform in size, $36.4\text{--}37.7\mu$ in diameter. Furrows more than three, irregular in arrangement but mostly representing imperfectly the configurations of the trischistoclastic system.

THALICTRUM Tourn. Meadow-rue

Grains spheroidal, of various size from 18 to over 30μ in diameter, without furrows but provided with 7–18 pores, the latter approximately circular, their membranes flecked with coarse granules, sometimes so copiously as to be almost obliterated by them, their margins smooth or with adhering granules. Exine finely but conspicuously granular.

These grains are similar to those of *Naravelia* but may be distinguished by their generally larger size and fewer pores.

The genus comprises about 76 species of slender branching herbs with ternately compound leaves and wind-pollinated flowers. Widely distributed in Europe, Asia, and America.

THALICTRUM DIOICUM L. Early meadow-rue (fig. 8). Grains uniform, about 18.5μ in diameter. Pores 6–10, prevaillingly, 6, tetrahedrally arranged their membranes heavily flecked.

A slender herb of moist woods, common in the northeastern United States and Canada.

THALICTRUM POLYGAMUM Muhl. Tall meadow-rue. Grains uniform, 22.5 – 25.5μ in diameter. Pores 7–9, various in size, circular or elongate in outline, when the latter occasionally triconvergent, their arrangement resembling that of furrows in the trischistoclastic system.

Native of the eastern United States and Canada.

THALICTRUM CLAVATUM DC. Grains extremely various; many of them dwarfed and obviously abortive. Normal grains about 28.5μ in diameter, but many apparently normal both larger and smaller. Pores about 15–18, uniform, their membranes copiously flecked.

Similar in appearance to early meadow-rue but flowers white and all perfect. Native of the eastern half of the United States, principally southward.

THALICTRUM DIPTEROCARPUM Franch. Grains somewhat various, 17 – 23.8μ in diameter. Pores 10–12, various, their number not correlated with their size or with that of the grain.

ADONIS [Dill.] L. Adonis

Grains generally uniform, ellipsoidal or spheroidal, 25 – 30μ in diameter, tricolpate. Furrows long and narrow, tapering to pointed or blunt ends, their membranes copiously flecked or encrusted with material resembling fragments of the exine, their margins rough. Exine thick and rigid, granular and slightly papillate.

Annual or perennial herbs with finely dissected alternate leaves and showy flowers.

Native of north temperate regions of Asia and Europe.

ADONIS AESTIVALIS L. Summer adonis. Grains ellipsoidal, deeply three lobed in outline with the furrows in the depressions. Furrows narrow, tapering to sharply pointed ends, their membranes heavily encrusted with a longitudinal strip of material resembling coarse-textured exine, almost completely demobilized. Exine finely granular and vaguely papillate, rather thick throughout and greatly thickened at the poles (umbonate).

The elongate form of these grains, which is generally maintained even when fully expanded, is due to the nearly complete demobilization of the furrows.

A commonly cultivated herbaceous perennial. Native of central Europe.

ADONIS VERNALIS L. Spring adonis. Grains uniform, spheroidal or slightly ellipsoidal, not three lobed. Furrows tapering to blunt ends, their membranes copiously flecked, but not heavily encrusted. Exine fine-granular, finely but distinctly papillate, thick but not further thickened at the poles (not umbonate).

These grains differ from those of *A. aestivalis* principally in the lack of encrustation of the furrow membranes, and the lack of umbonate thickenings at the poles.

A commonly cultivated herbaceous perennial, native of central and southeastern Europe.

While this paper was in the hands of the publisher there appeared an article on the same subject (Kumazawa, M. 1936). It is unfortunate that this work came to my notice too late to receive adequate consideration, since the author describes and illustrates the pollen grains of many of the species treated here. Dr. Kumazawa's findings and mine are substantially in agreement; particularly noteworthy is this author's conclusion that the pores of the pored grains represent proliferated and shortened furrows.

Yonkers, N. Y.

Literature cited

- Kumazawa, M. 1936. Pollen grain morphology in Ranunculaceae, Lardizabalaceae and Berberidaceae. Japanese Jour. Bot. 8 (1): 19-46.
Wodehouse, R. P. 1935. Pollen Grains. The McGraw-Hill Book Co., Inc., New York.

Explanation of plate 20

Fig. 1. Pollen grain of *Paeonia albiflora*, approximately in polar view, 34μ in diameter.

Fig. 2. Pollen grain of *Calltha palustris*, approximately in polar view, 25μ in diameter.

Fig. 3. Pollen grain of *Coptis trifolia*, 18μ in diameter.

Fig. 4. Pollen grain of *Aconitum delphinifolium*, approximately in polar view, 25μ in diameter.

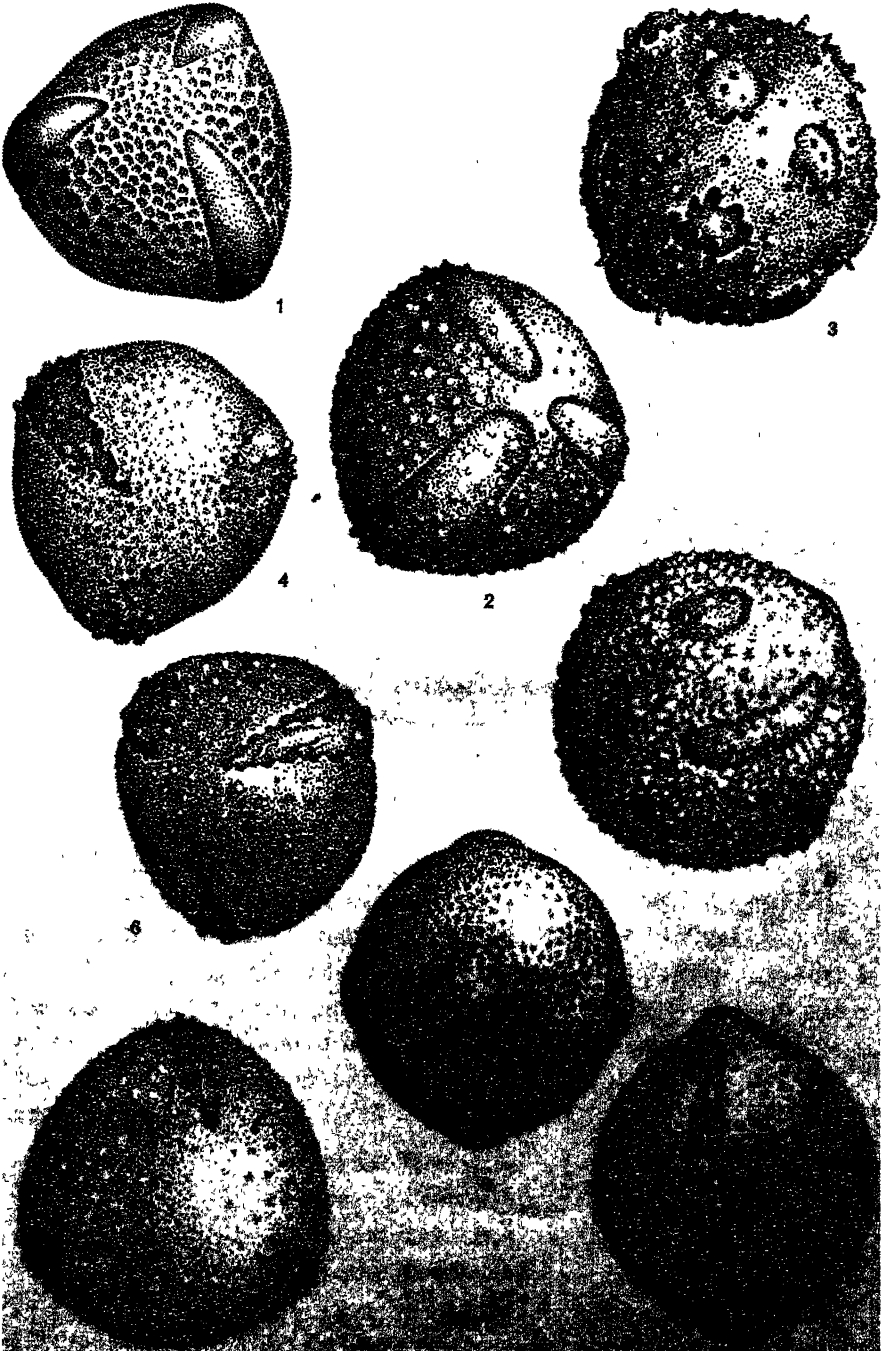
Fig. 5. Pollen grain of *Syndesmon thalictroides*, 40μ in diameter.

Fig. 6. Pollen grain of *Clematis montana*, approximately in polar view, 22μ in diameter.

Fig. 7. Pollen grain of *Ranunculus abortivus*, approximately in polar view, 25μ in diameter, chosen as the type of the family.

Fig. 8. Pollen grain of *Thalictrum dioicum*, 18.5μ in diameter.

Fig. 9. Pollen grain of *Adonis aestivalis*, side view, 28μ in diameter.



The tolerance of liquid air temperatures by dry moss protonema

CHARLES B. LIPMAN

(WITH ONE TEXT-FIGURE)

In two earlier communications^{1,2} the writer has demonstrated that many kinds of seeds and bacterial and fungus spores can withstand without injury the temperatures of liquid air and even those very close to the absolute zero ($1^{\circ}.3$ K.). Tolerance of liquid air temperatures and lower temperatures by seeds had been demonstrated by others, and my work confirms that and extends it, in that I proved that exposure to liquid air for sixty days is as well tolerated as exposure for a few hours. The evidence which I presented on the tolerance of so low a temperature as $1^{\circ}.3$ K. was, however, a record for low temperature tolerance by seeds and bacterial spores which, so far as I was aware at the time the results were published, had not been approached by other investigators. Recently I have found that similar results, but perhaps at slightly higher temperatures, were obtained by Becquerel, but I did not become aware of his results until after I had completed the experiment which forms the subject of this paper and which confirms, and is confirmed by Becquerel's results of a similar nature.

It will have been noted that, in the experiments with seeds and spores, we were dealing entirely with resting stages of organisms. It seemed to me highly desirable to determine whether or not vegetative tissue in any form was possessed of tolerance to such low temperatures as that of liquid air. In reflecting on the kind of vegetative tissue which might lend itself well to experimentation for such a purpose, I thought of moss protonema as probably the most promising material. I was moved to this conclusion by the well-known tolerance to desiccation and to wide temperature ranges which characterize mosses. About that time an article by Professor Conard of Grinnell College on the mosses of Iowa came to my attention, and I ventured a request to him for samples of different species. I requested samples of vegetative tissue or non-fruitlet species. Professor Conard was gracious and generous enough to send me small specimens of the following species of mosses:

Dicranella heteromala

Hypnum patientiae

Dicranum scoparium

Bartramia pomiformis

¹ Lipman, Charles B., and Lewis, G. N. Tolerance of liquid air temperatures by seeds of higher plants for sixty days. *Plant Physiol.* 9: 392-394. 1934. *

² Lipman, Charles B. Normal viability of seeds and bacterial spores after exposure to temperatures near the absolute zero. *Plant Physiol.* 11: 201-205. 1936.

Thelia asprella
Entodon seductrix
Brachythecium cyrtophyllum
Catharinea angustata

Professor Conard stated that *Hypnum patientiae* and *Entodon seductrix* never fruit in Iowa, and that the others showed no signs of fruiting when the specimens were collected. They were all collected nine miles southwest of Grinnell, Iowa, in Jasper County.

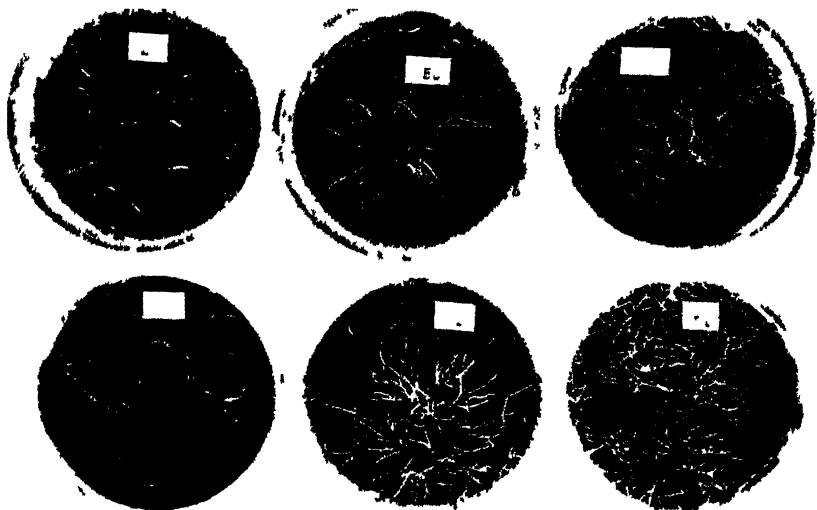


Fig. 1. Photograph of three of the treated mosses and controls. Reading from left to right:

Hypnum patientiae
Thelia asprella
Brachythecium cyrtophyllum

Top row control specimens, only dried in vacuum. Lower row treated specimens, fifty hours in liquid air. Specimens all growing in soil in tumblers.

The specimens reached me on October 8, 1935. Being occupied at the time, I set the specimens aside in the dry condition in which they arrived in tissue wrappings. They remained thus until December 26, 1935, when they were placed in a desiccator over sulphuric acid, and the desiccator was evacuated. The specimens remained in this dry vacuum until February 14, 1936, when they were removed and treated as follows: Each specimen, though very small (about half an inch to an inch in diameter) was

divided into two. One of the halves was placed in a Pyrex tube, and the tube was sealed. The other half was saved for a control. The samples of the different species thus prepared in sealed tubes were immersed in liquid air and kept there for fifty hours (temperature approximately -190° C.). At the end of fifty hours the specimens were removed from the sealed tubes, and each was placed in a beaker of tap water. The controls were likewise placed in beakers of tap water. All the specimens remained in the beakers from February 20-24, 1936. Within a few hours it was evident that all the moss specimens, both the controls and treated, had swelled markedly, and microscopic or other examination showed the cells to be perfectly normal, the chloroplasts in good condition, and apparently none the worse for the long and very rigorous drying, or the liquid air exposures in the case of the treated samples. After four days in the tap water, the mosses were removed to the surface of moist and properly prepared soil in tumblers. Fungi had attacked them all in the tap water, and some of the samples were beginning to disintegrate. In spite of that, three of the eight species survived the attacks of the fungi, and are growing very well to this day (July 15, 1936). A photograph showing control and treated specimens of these three species accompanies this paper. The other species were so injured by fungus attack that they died. It will be noted that the controls, as well as the treated specimens, died in this manner. It is fortunate that one of the species which survived the attacks of the fungi was *Hypnum patenitiae*, which, as Professor Conard reports, never fruits in Iowa. There can certainly be no question of surviving spores, in this case, having been responsible for the growth obtained.

The foregoing experiment leaves no doubt that the protonema of moss in a dry state can withstand the temperature of liquid air as well as seeds do, and as well as spores of bacteria and fungi, as the writer in common with others, proved earlier. An examination of the photograph which accompanies this paper will satisfy the reader that the mosses treated, as well as untreated, are growing actively and producing new and healthy shoots. I stated above that, after I had completed this experiment, there came to my attention the recent work of Becquerel, which my experiment confirms. I did not learn of the report of Becquerel's work on mosses, in very brief form, until I saw the Proceedings of the Sixth International Congress of Cryoscopy held at Buenos Aires in September, 1932. Soon thereafter, I learned of Becquerel's report to the International Botanical Congress held at Amsterdam in September, 1935, which in the Proceedings of that Congress gives another very brief account of experiments with seeds and spores near the absolute zero, but does not mention any further work with dried vegetative tissue. I shall have occasion to refer, in another

paper bearing on related experiments, to other phases of Becquerel's work and to experiments of others of a most striking nature. It is pertinent in this connection, however, only to point out that Becquerel's work on mosses and mine are mutually confirmatory. Moreover, Becquerel's generalization from his experiment with mosses and from his other low temperature experiments, relative to the absence of respiration in organisms kept at very low temperatures, is in entire agreement with my own. Several years ago in a paper read before the National Academy of Sciences at a meeting held in Berkeley, I gave an account of my discovery of living bacteria in anthracite coal, in which I stated as one conclusion my belief that spores of bacteria might exist in rocks or in other old forms of matter in a non-respiring state which I called "suspended animation." In my papers to which I referred above, I gave the definite proof of the correctness of my earlier conclusion. I find now that in the brief account of Becquerel's discussion before the International Botanical Congress at Amsterdam, he uses exactly the same term as I used several years ago. It is gratifying to me to have arrived quite independently at the same conclusion as Becquerel respecting this important matter. Since I shall have more to say elsewhere on "suspended animation," I need say nothing further about it here, except that moss protonema can apparently stop respiring without losing its power to live at some later time under the proper conditions, just as several of us have proved that seeds and spores can do, and this further emphasizes the correctness of my conclusion that the property of life depends not on a reaction, but on a pattern or design of matter. It is unthinkable that respiration can go on either at liquid air temperatures or at the absolute zero, when all the materials and conditions necessary to respiration are effectively absent.

To Professor H. S. Conard of Grinnell College, who furnished the moss specimens for this experiment, to Professor C. W. Porter of the Chemistry Department of the University of California, who supplied the liquid air therefor, and to Mr. W. L. Chandler, who assisted me with the laboratory work, I acknowledge my grateful indebtedness.

UNIVERSITY OF CALIFORNIA,
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An international system of botanical districts¹

CARL O. GRASSL

My interest in plant geography has convinced me that if we are to advance efficiently in this science it will be necessary to standardize our main concepts and procedures. With this idea in mind I am proposing for the consideration of collectors and herbarium students some innovations in the manner of recording phytogeographic data.

The crying need for a serviceable subdivision of the earth's surface into botanical districts leads me to suggest that we make use of small quadrangles limited by meridians and parallels, the unit botanical district to be a square degree. In other words, the areas bounded by whole degrees of latitude and longitude should be recognized as botanical districts.

Such a system of botanical districts would divide the surface of the earth into 64,800 distinct rectangular units one degree on a side. Actually we would not be very much concerned with many of these, as much of the earth is covered by oceans or ice-fields on which, for the most part, plants are not to be expected. A rough estimate indicates that about twenty thousand of these areas play a part in the distribution of the higher plants. That twenty thousand or so unit districts is not an unreasonable number will, I hope, become clearer as the advantages of the system are pointed out.

In order to facilitate the comparison of the proposed system with any others that may come to mind, I have listed the main reasons that have led me to believe this system the best. The reasons dealt with below, are not necessarily in the order of their importance.

CONVENIENCE AND SIMPLICITY OF THE UNIT

A "square degree," the unit of the proposed system of botanical districts, can be represented in a manner which is very convenient and yet be immediately understandable to all students of science throughout the world. For example, the district in which Ann Arbor, Michigan, is situated might be represented thus: 42-3N83-4W, meaning the area between 42° and 43° North Latitude, and between 83° and 84° West Longitude. This short way of designating a district could be even more abbreviated, i.e., to 42N83W, if it was understood that an area was meant rather than a point. For most purposes the slightly longer but customary way of indicating an area is preferable.

The areas represented by quadrangles of a square degree are reason-

¹ Papers from the Department of Botany and Herbarium of the University of Michigan, No. 593.

ably uniform in size and shape. The only appreciable variation that occurs is in longitude as one goes towards the poles. This is because a degree of longitude varies from about 70 miles at the equator to zero at the poles. Inasmuch as this variation is in width only (the variation in latitude being less than 1%) and since it is not appreciable between neighboring units; it can for most purposes be disregarded. This is especially true since the districts which are most affected lie near the poles and consequently do not concern us very much. In studies where it is desirable to compare equal areas which are widely separated in latitude, such as arctic regions with tropical ones, it is only necessary to make use of the flexibility of the system as indicated below. For example several neighboring arctic districts could be lumped together thus: 81-2N45-8W, to obtain an area almost equal to a single unit near the equator.

The areas which these districts represent are of a convenient size. An average district will be about 50 miles wide and 69 miles long. Another way of realizing their size is to consider that the United States contains about 900 such units. The size of these units is convenient because it is large enough so that the areas may easily be found on small scale maps and yet is small enough to serve as a basis for local floristic studies.

The principal advantage of having such uniform and therefore comparable districts is that it will simplify treating the major problems of plant distribution. As soon as we possess data for numerous comparable units it becomes a simple matter to recognize similarities and differences between them and from these to draw valuable conclusions. Uniform units will enable us to construct zones of vegetation which are actually based upon the complex of plant distribution rather than as at present, upon compromises and guesswork. In other words, the use of a fundamental unit is necessary for precision in the comparison and subordination of phytogeographic data.

FLEXIBILITY OF THE SYSTEM

A system of districts based upon meridians and parallels, and having as its unit a square degree, has the great advantage of being flexible, inasmuch as areas of a larger or smaller size are readily formed by grouping or subdividing them. The ways in which this could be utilized are numerous and important, and consequently will be dealt with in some detail.

Starting with the subdivisions, we find that the most important and usable modification would be the addition of minutes of degree as a means of indicating the approximate locality at which a collection was made. This would fit in excellently with the above system of districts as it would enable us to change at will the size of the units upon which we were basing

our distribution studies. Application of this modification appears imminent as it is becoming more obvious every day that locality references, if they are to be usable, must be qualified by degrees and minutes of latitude and longitude.

The question as to how plant localities should be recorded on the labels of plant collections and in floristic and monographic reports is becoming more important with every increase in the number of collections and in the accuracy with which they are localized. A satisfactory solution to this problem must take into consideration various factors. To be successful, a method of recording plant localities must not only be practical as far as the collector is concerned, and therefore based upon the best maps available, but must be readily understandable and usable by museum students. Undoubtedly the most logical and satisfactory method of accomplishing this is by qualifying, in terms of degrees and minutes of latitude and longitude rather than in terms of political units, the exact locality at which a collection was made. This would mean that instead of saying that a collection was made at a given spot, at a given distance and direction from a recognizable city, in a given county, of a given state, we would stress and improve the accuracy of the information about the exact locality, and describe its approximate position in terms of the nearest meridian and parallel. The growth of cities, and the frequent changes and duplications in place names and political units, makes any system based upon them temporary and provincial if not actually impracticable.

It would be well indeed, if we could localize our collections even more accurately, as for instance, to seconds of a degree; but since our present maps do not permit this, localization has to be realized in another way. To find (probably many years later) practically the identical spot at which a collection was made, I have designed a field label (see fig. 1) with a rectangle in the upper right corner to represent a map of the area from which the collection was taken, the size and shape of the rectangle determined by the grid of the base map. If practicable, the rectangle should represent a square minute or fraction of a minute of degree. Generally, however, the rectangle will have to be based upon a map in which the subdivisions represent public-land divisions. Whatever the rectangle represents should be indicated upon the field label. In figure 1, the rectangle (in this instance a square) represents a public-land division of one square mile in extent known as a section and commonly shown on United States topographic and soil maps. Suitable blank spaces in which to indicate which section is meant and the township (distinguished by township and range numbers rather than by name) in which it occurs have been provided on the label. By carefully marking the square not only can we indicate (with an error

of only a few hundred feet) the spot at which a collection is made, but also the distribution of the species with respect to the topography, soil, and other edaphic factors. A triangle could be used to designate the spot at which the collection was made, while plus and minus signs could be used to indicate the presence or absence of the species as far as the observations

PLANTS OF MICHIGAN	
.....° ' N. Lat.,° ' W. Long.	
T..... R..... Sec.....	
C. O. Grassl, no.....	
Date....., 193.....	
Locality.....	
.....	
Habitat.....	
.....	
Dispersion & abundance.....	
.....	
.....	
Special characteristics & notes.....	
.....	
.....	
.....	

Fig. 1. A field label for use in the United States. The square in the upper right corner represents a section (one square mile). Actual size 5 by 3 inches.

permitted. It is only by some such method that collectors can prepare collections with permanent phytogeographic as well as taxonomic significance.

I have purposely planned a small label (5 by 3 inches) so that a pad of them may conveniently fit into one's pocket and also so that they may

serve in emergency as ordinary herbarium labels. When it is desirable to take more copious notes than the few blank lines allow it is only necessary to use the back of a second label. If one wishes a separate herbarium label the field label can be shortened to 4 inches by eliminating the space for the Latin name.

It is unfortunate that so few collectors use field labels. As E. D. Merrill² has often pointed out, there can generally be no serious objection to the use of field labels. On the contrary, they enable the conscientious collector to work much more efficiently and accurately than is possible without them. Probably the main reason why many collectors avoid the use of field labels is their inability to apply them to the outmoded ways of collecting with a vasculum or some similar equipment. Why anyone should use a vasculum when many more and much better specimens can be obtained by collecting directly into a press (with shoulder straps if so desired) is not understandable.

The expense of field labels is not a valid objection to using them, for it is better to retain a field label as a permanent herbarium label than it is to dispense with a field label because generally more expensive herbarium labels are to be printed later.

Returning to the uses of subdivisions, it would turn out that students in the relatively more botanized districts, such as the New England States, would find a square degree too large a unit. Then $\frac{1}{4}$ or $1/16$ of a square degree would be a convenient area on which to base local studies, since topographic maps at least in the United States are prepared, for the most part, on that basis.

When we consider the many possible ways of combining degree units to form larger areas we find many more advantages to our system. Regions of five or ten degrees on a side might very well be considered as suitable areas for more comprehensive floristic work. Such groupings could be made much more natural and comparable than the political ones now used.

Another way in which large aggregates of unit districts could be made use of is in the segregation of herbarium sheets. For this purpose there are any number of possible arrangements all based upon the same principles of numerical progression in longitude and latitude. The size of the steps of latitude and longitude used for each folder could be based upon the range and abundance of particular species. Within the folders representing the major groupings any degree of refinement in arranging the sheets could be accomplished. Some such system would greatly facilitate her-

² Merrill, E. D. On the utility of field labels in herbarium practice. *Science*, N.S., 44: 664-670, 1916. The significance of the compiler's data in field work. *Bull. Torrey Club*, 61: 71-74, 1934.

barium research and would eventually be practicable if some of the other suggestions made above were ever realized.³

Still another use for such districting as I have suggested would occur whenever accurate regional bibliographies or abstracts of regional reports were to be prepared. The ease with which meridians and parallels could be used to indicate and index the exact regional significance of a report would greatly simplify bibliographical problems.

INTERNATIONAL IN SCOPE

Finally we have the fact that districts based upon meridians and parallels have permanent boundaries and are international in scope. This will greatly aid us in the tremendously important work of accurately mapping the distribution of species throughout the world. Because of the great regularity exhibited by districts of a square degree, uniformity in the manner of mapping will be relatively easy to accomplish. Uniformity in the manner of mapping the distribution of species can be further increased, by setting up suitable criteria based upon the number of distinct stations and their position within the districts.

It is unfortunately true that, in spite of the fact that the meridian of Greenwich has been universally accepted as the initial meridian, most topographic maps of foreign countries are still based upon local meridians. The Portuguese, for example, use the meridian of the Naval Observatory in the Royal Park at Lisbon ($9^{\circ}11'10''$ West of Greenwich). This is not an important obstacle, however, as it is very easy to change a longitude so that it is based upon Greenwich. A collector in Portugal would only have to add $9^{\circ}11'10''$ to each longitude to base it upon Greenwich. If on the other hand one was collecting in France, it would only be necessary to subtract $2^{\circ}20'14''$, since Paris (Obs. nationale) $2^{\circ}20'14''$ East of Greenwich is there used as the prime meridian. In a similar manner allowance could be made for any local meridian now in use.

Summing up the arguments for a system of botanical districts based upon the square degree we find that it would be advisable because of its simplicity, flexibility, and practicability. Evidence indicating its workableness has been obtained in the field and herbarium study for a report that I am preparing on plant distribution in the northern Great Lakes Region.

DEPARTMENT OF BOTANY
UNIVERSITY OF MICHIGAN

³ For other ways in which botanical districts of a square degree can be made use of in herbaria see the writer's article "Visualizing our herbaria by the application of mechanical methods of tabulating and indexing." *Museums Journ.* (in press).

On the classification of *Euphorbia*. I. How important is the cyathium?

LEON CROIZAT

A century and a half of controversy has left it undecided whether *Euphorbia* L. is a single genus or a group of genera. The quarrel of the Linneists and Anti-Linneists¹ has been fought to a standstill, with the Linneists at present more numerous. In itself the issue is older: its roots are in the works of the herbalists who saw a distinction, rejected by Linnaeus in all his works, between *Chamaesyce* and *Tithymalus*, *Euphorbium* and *Peplis*.

As presented by either school the classification of *Euphorbia* or of the genera segregated from it challenges an impartial observer. The Linneist stands by a generic definition two centuries old which assumed that the cyathium is a flower. The major premise of this definition has been proved false: the cyathium is an *inflorescence*, not a flower. One must wonder whether a notion fundamentally erroneous can become fundamentally true. Furthermore, the Linneists too easily surrender the right to understand and to interpret facts that bear vitally upon classification. Says Boissier (D.C. Prodr. 15²: 8. 1862), "The characters of the sections are often trifling and open to exception but *better ones can not be found*" (translation and italics mine). N. E. Brown writes (Fl. Trop. Afr. 6¹: 471. 1911), "The spines of succulent species in books have been called 'stipular spines', but as they are always developed below, and sometimes at a distance below the leaf or the leaf-scar, they cannot be stipules in the ordinary sense of that term; *what their real relation to the leaf is I do not quite understand*" (italics mine). No one familiar with these and like statements feels surprised in finding that the "sections" of *Euphorbia* are *nomina nuda* or without precise definitions. In fact the same "section" includes species with or without "stipules," with or without a definite main axis, and with or without a terminal inflorescence, and digests without difficulty species that are glaringly unrelated. However, such "sections" are a lesser evil than the blank classification of some Linneists. The works of these taxonomists scarcely exceed the value of a catalogue or of a collection of descriptions; their secrets are sealed except to the peering eye of profound hierophants.

The classification of the Anti-Linneists is fundamentally negative. It repudiates as a matter of course the "unnatural union of the spotted

¹ By "Linneists" are here understood the botanists who believe *Euphorbia* L. to be a single genus, by "Anti-Linneists" those who take the contrary view. The terms are used for brevity, and are not derogatory.

spurge and of the garden caper" (Eaton, Man. ed. 2. 243. 1818), but seems incapable of producing generic definitions that precisely apply to one harmonious group of species and interpret the structures that puzzle the Linneists. The weakness of the Anti-Linneistic definitions is trifling compared with the tendency inherent in the concepts of the school to introduce monotypic genera based upon the study of a limited flora. Nothing is gained in the adoption of principles that segregate one species from two thousand.

Both systems of classification, then, are stultified by a hidden inconsistency, and blighted by a false start. If the definitions of the genus and of the genera are unsatisfactory the trouble plainly lies in the concepts.

The Linneists and the Anti-Linneists appear to differ fundamentally in this: The Linneists believe that *cyathium* and *Euphorbia* are synonymous, or very nearly so, and refuse to admit the validity of differences in habit, spines, stipules, and the like. Their position, bluntly stated, is one of conservatism hallowed by tradition. The Anti-Linneists lay stress on the differences in habit, spines, sizes, stipules and the like, and claim that these differences are weightier than the mere possession of a *cyathium*. Their position is difficult, for they must produce proofs and overcome the authority of standing classification.

We have defined the issues. Let us, this being done, take the concepts of the opposing schools and reduce them to their fundamental thesis. We hear:

- a) The *cyathium* is not *the* generic character of *Euphorbia*.
- b) the *cyathium* is *the* generic character of *Euphorbia*.

From 1870 on all botanists have agreed that the *cyathium* is an inflorescence. Accordingly we substitute equivalents, and have;

- a') the inflorescence is not *the* generic character of *Euphorbia*.
- b') the inflorescence is *the* generic character of *Euphorbia*.

The substitution of *inflorescence* for *cyathium* takes the issue out of the narrow circle of the "specialists" and brings it for a verdict to the common run of botanists who all know how *inflorescences* are treated in taxonomy. Five questions follow.

The first question is addressed to the Anti-Linneists: what in their concept, is the generic character of the various groups of species they segregate from *Euphorbia*?

The answers are many and should be analyzed in detail, were not this paper concerned with principles. The Anti-Linneists more or less soberly agree that the *cyathium* is important in its parts if not as a whole: they postulate appendages, glands, seeds, and to a lesser extent, perhaps, "stipules" and phyllotaxis. If the writer be correct, Ch. Lemaire single-

handed proposes a concept that is reminiscent of the evolutive interpretation of groups of species (cfr. Observations on *Anthacantha*, Ill. Hort. 2: Misc. 68, 1855; 5: Misc. 64, 1858). It is evident that most if not all of the Anti-Linneists still believe in the cyathium, and wage mere verbal warfare against the Linneists. C. F. Millspaugh, a name to conjure with in certain parts of the world, undoubtedly has much in common with Rafinesque, at least with Rafinesque in a sober mood, and there is a suspicion that the extreme conservatism of many an American taxonomist expresses a psychological reaction to the Rafinesquian and Millspaughian serenades. Klotzsch is vastly more ambitious than Necker but not better informed; Boissier castigated him, and the botanists of Europe, mayhaps, still fear the shadow from Geneva.

The Linneists are positive or very nearly positive that where there is a cyathium there stands *Euphorbia*. Their position is clear, and invites precise questions. Three will be asked of them:

1st) Does the inflorescence of *Euphorbia* belong to a group of species that are alike in degree of evolution?

The answer is no. Some species have interpetiolar stipules, others glandular stipules; some are annual, unarmed herbs with opposite leaves, others biaculeate perennial trees with reduced alternate leaves. The "spines" result from spinescent branches as in *E. lignosa* and *E. triaculeata*, from dried persistent floral peduncles as in *E. polygona*, from the operation of a process to most authors wholly unintelligible as in *E. antiquorum* and *E. Cooperi*. Beyond these differences, furthermore, the Linneist recognizes a fundamental likeness among the species of certain groups. Hence the "sections," and the admission that, after all, an *Anisophyllum* is not a *Tithymalus*, even though a *Trichosterigma* may be anything having "petaloid" appendages, and *Goniostema* can nurse on its capacious bosom half the species of Madagascar.

2nd) Does the inflorescence of *Euphorbia* L. belong to that genus alone?

The answer is no. An inflorescence in which certain members (bracts or scales) become adnate to form an involucre for the flowers, basically a cyathium, belongs to at least seven genera that are accepted in the seats of orthodoxy, and to fifty or more genera devoutly believed in by less orthodox botanists. Pax, whose concepts coincide with those of Engler's Pflanzenreich and may not be suspected of heterodoxy, rejects *Pleuradena* (*Poinsettia*) but indorses *Diplocyathium*, *Anthostema*, *Dichostema*, *Calycopeplus*, *Euphorbia*, *Elaeophorbium*, *Synadenium*, *Monadenium*, *Stenadenium*, and, it seems, *Tithymalus* (*Pedilanthus*). Pax states that the cyathium is the main character of *Euphorbieae*, not of *Euphorbia* (Bot. Jahrb. 59: 151, 1924) which somewhat agrees with N. E. Brown's statement

(Fl. Trop. Afr. 6¹: 471. 1911) to the effect that, "in a few of the teretestemmed and spiny succulent species [of *Euphorbia*] the involucre-glands are united into one continuous rimlike gland or with only a faint indication of lobing; in these there is nothing but habit to separate them technically from *Synadenium*." So great is the authority of Boissier and Pax, however, that N. E. Brown indorses *Synadenium* without further qualification.

3rd) Is the inflorescence of *Euphorbia* an anatomic constant: that is, are its flowers and their involucre anatomically alike, and constant, in all the species of the genus?

The answer is no. The involucre may have a peculiar shape (*E. pedilanthoides*), colors that exceed the limit of the cyanic and of the xanthic series, hard texture (*E. sclerocyathium*) and a greater or lesser degree of adnation to the axis that supports the female flower as in most *Euphorbiae* sect. *Anthacantha*² and in *E. virgata*. The nectarium (the writer prefers this term to the commonly used "gland"), and its appendages vary bewilderingly (*E. leucodendron*, *E. Antso*, *E. fulgens*, *E. clavidigitata*, *E. pauciflora* Duf., *E. pauciflora* var. *pectinata*, *E. cinerascens*, *E. noxia*, *E. Caput-Medusae*, *E. biglandulosa*, *E. corollata*, *E. antiquorum*). The male flowers mostly have staminodia in *E.* sect. *Diacanthium* and are generally without them in *E.* sect. *Tithymalus*; they are fascicled in Indian species of sect. *Diacanthium*, more or less irregularly arranged in curls in other species; free, or partly or wholly surrounded by septa from the involucre (*E. fulgens*, *E. splendens*). The ovary, usually 3-locular, is distinctly 2-locular in *E. Intisy*, and mostly 2-locular, although evidently by abortion in *E. bilocularis* and *E. tetraptera*. The styles are usually discrete, subulate and entire in *E.* sect. *Goniostema*, connate to various heights, lobulate and cleft in *E.* sect. *Tithymalus*. The mature capsule is variously winged or armed (*E. tetraptera*, *E. cybirensis*), indehiscent (*E. akenicarpa*), or projectile (most herbaceous species). The epicarp is fleshy (*E. abyssinica*, *E. pachysantha*), spongy (*E. Lathyris*), or dry (most species). The seed is more or less thickly arillate (*E. Chamaesyce*, *E. Peplis*), carunculate (*E.* sect. *Tithymalus*), ecarunculate (*E.* sect. *Anisophyllum* and sect. *Diacanthium*). These variations are but a few of the many that a careful check of all the known species would reveal.

The answer to the above questions leaves the cyathium of *Euphorbia*, and of the genera segregated from it, in a position which is unmatched by that of any other inflorescence in taxonomy. This peculiar inflorescence belongs to many genera but is commonly used to define precisely only one;

² The "sections," here introduced for the sake of brevity, are taken from Boissier in D. C. Prodr. 15²: 7-187. 1862, and from Pax in Engler, Veget. Erd. 9: 1-168. 1921.

it is not subject to the rules that govern other inflorescences in botanic interpretation; it fails certain genera (cfr. note of N. E. Brown on *Euphorbia* and *Synadenium* (o.c., l.c., quoted above)) but, then, the habit of the plant takes its place; it reunites species that are unrelated in degree of evolution; it is not anatomically constant either in its parts or in the flowers it contains, but the characters derived from its variations are powerless to delimit clearly defined genera.

What, then, is this cyathium? What is its value in taxonomy?

What the cyathium really is we shall soon see. Its value in taxonomy can be judged by the results it yields and by the method it forces upon those who elect it, in whole or in part, as *the* generic character. We see that the cyathium is a myth, a wholly unnatural character, like the drupe or the corolla that in the works of the *artificial* classification defined unrelated groups of plants, *fructu drupaceo donatae* or *corolla papilionacea praeditae*. The cyathium has its place in the works of Tournefort and of Linnaeus: it can not alone serve modern botany, and that is not surprising if one remembers that modern botany claims to be natural and that the cyathium is an inflorescence, not a flower.

So far in principle. In practice the untenable position into which the cyathium-myth forces the Linneists, who fundamentally use it as a flower, and the Anti-Linneists who pull it apart in search of "floral characters" can be shown in Pax's *Die Phylogenie der Euphorbiaceen* (Bot. Jahrb. 59: 129-182. 1924.) This work is considered a classic and it makes abundantly clear that the cyathium-myth is inconsistent with scientific interpretation generally, least of all with a natural system of classification.

In 1907 H. Schmidt proposed the monotypic genus *Diplocyathium* based on *E. capitulata* Reich. The species is *prima facie* a member of sect. *Tithymalus* (cfr. Reichenb. Icon. Flor. Germ. Helv. 5: 1841 fig. 4759a, pl. cxxxvi.) The genus, however, is strictly "orthodox": the species constantly has a double or multiple involucre, and nectaria (glands) to fit the number of involucres.

According to Pax (o.c., 151), the understanding of the phylogeny of *Euphorbieae* requires that the proper value be placed upon *Diplocyathium*. The multiple involucre of the type may be considered a specific character, and it may be asked how the structure came to be. Abnormalities in the cyathium are in the record, but since *E. capitulata* constantly exhibits a multiple involucre *Diplocyathium* must be considered valid. Thus is *Diplocyathium* an archetype. In obedience to these principles Pax draws a phylogenetic tree in which *Diplocyathium* is separated, graphically, at least, from *Euphorbia* by *Anihostema*, *Dichostema*, and *Calycopseplus*, and is shown to be farther remote from *Euphorbia* than *Stenadenium*.

The concepts underlying Pax's understanding of the matter do not come in for discussion here. The nomenclatural validity of *Diplocyathium* might be admitted because the earlier *Diplocyathia* N. E. Brown (*Diplocyathius* K. Schum.) belongs to Asclepiadaceae. It is questionable if not reprehensible, however, that Pax accepts *Diplocyathium* and rejects, e.g., *Epurga*, and neglects the "orthodox" genera required by *E. pedilanthoides* and *E. sclerocyathium*. Furthermore: in phylogeny *E. palustris* might be more interesting than any of the species mentioned: its ovary exhibits peculiar facts (cf. Ber. deutsch. bot. Gesell. 29: 430-436. 1911.) Once the way is clear, in the name of orthodoxy Rafinesque's "species-genera" must be outdone.

A natural classification must not use artificial characters. If *E. capitulata* is an archetype and it can with reason be assimilated sooner to *Euphorbieae* from Africa and Australia, than to *Euphorbia*, its unique position must be supported by an evidence stronger than a double or multiple involucre. But for this, it has been noticed, *E. capitulata* takes rank within sect. *Tithymalus*.

E. capitulata is reported from the high mountains of Dalmatia, Albania, Jugoslavia. This range stood as a zone of refuge during glacial quaternary times, and, as one expects, is rich in species and in forms that exhibit ill defined characters, or are strictly endemic (*E. veneta*, *E. Tommasiniana*, *E. flicina*, *E. dalmatica*, *E. triflora*, *E. Jacquinii*, *E. epithymioides* (*E. fragifera* Jan.) The affinities of the species are with *E. Schottiana* (Cilician Taurus) and it seems, with *E. monocyathium* (Altai, Trans-Altai, Pamir). Its floristic status is precisely the status of *E. herniariaefolia* (Greece to Mesopotamia), *E. caudiculosa*, *E. bounophila*, *E. Aucheri*, *E. Kanaorica* (Asia Minor to India), *E. Valliniana*, *E. ventosica* (Western Alps), *E. chamaebuxus*, *E. pauciflora* (Pyrenees). The axis of range *E. capitulata*—*E. Schottiana* is very nearly parallel to the axis of the range *E. Broteri*—*E. pectinata*; *E. taurinensis*—*E. sareptana*; *E. nicaeensis*—*E. tinctoria*; *E. glebulosa*—*E. dracunculoides* etc. In brief: *E. capitulata* is an alpine relict, a floristic aspect by no means uncommon in the flora of Europe, Northern Africa, Western Asia, which is still largely dominated by the fact of quaternary glaciations. Only an artificial character can assimilate *E. capitulata* to anything but to *E.* sect. *Tithymalus*. The species is a recently fixed one, not an archetype.

In the present state of the question the writer admits to prefer the concealed agnosticism of Boissier to the strictly "orthodox" yet palpably false assumption of *Diplocyathium*, and to the attempts at generalization that assume that the Linnean genus must be a "good" genus. This genus is "good" or "bad" not because one wishes it, but because the facts, and

an interpretation of the facts in harmony with the basic assumption of natural classification prove it to be true or fictitious. The record conclusively shows that much spade work remains to be done in order that the full implication of the concepts of the classification now in use can be grasped. Not all the facts have been found, and it is certainly difficult to find them. It is unfortunate that no monographic work is later than Boissier's treatment arranged *seventy-five years ago*. Taxonomists working in their own floristic domain may not be expected to compare a species, e.g., of Brazil with the species of Somaliland, Indochina, Australia and the Hawaiian Islands for the sake of deciding whether, fundamentally, Millspaugh is right in postulating *Chamaesyce*. For three quarters of a century the label "*Euphorbia*" has very conveniently gathered in hundreds of species separately presented which fell in with the Boissierian understanding and the Linnean definition because they exhibited a cyathium. Use and necessity, however, are not the criteria by which the truth of a postulate can ultimately be gauged.

Seven American melastomes

H. A. GLEASON

Meriania Simsiana Gl. sp. nov. Lignosa ubique glabra; internodia superiora 1 dm. longa superne paullo incrassata tenuiter alata, alis usque 2 mm. latis; folia sessilia verisimiliter amplexentia membranacea ovato-lanceolata, usque ad 28 cm. longa 12 cm. lata, acuta, integra, inferne late rotundata ad basin cordatam, sinu angusto, 7-plex-nervia, jugis 2 externis basalibus in lobos decurvatis, jugo superiore 15 mm. ultra basin folii oriente; venae secundariae supra obscurae subtus rubro-brunneae subplanae, e costis sub angulo fere recto divergentes; venulae tertiariae numerosae reticulatae; panícula terminalis 15 cm. longa multiflora, axi anguste alato; pedicelli circa 2 mm. longi; flores 5-meri; hypanthium obconico-campanulatum 8.5 mm. longum; calycis tubus 2 mm. longus, lobis late rotundatis 0.5 mm. longis; petala immatura; filamenta immatura latissima; antherae fere 8 mm. longae, connectivo ad antheram adnato crassissimo truncato fere 4 mm. longo; ovarium liberum 10-costatum.

Type, *Rimbach 211*, collected at (or between?) Chimbo and Balsapampa, Ecuador, alt. 2600 m., and deposited in the Britton Herbarium. The species is a member of the section *Pachymeriae*, and differs from the other species in its sessile plex-nerved leaves with cordate bases.

Graffenrieda trichanthera Gl. sp. nov. Arbuscula 3 m. alta; rami crassiusculi cinerei glabri, cortice sicco ruguloso; petioli crassi glabri, usque 10 mm. longi; laminae coriaceae lanceolatae, maximae usque 135 mm. longae 37 mm. latae, minimae terminales 45 mm. longae 17 mm. latae, omnes acutae integrae basi rotundae glabrae sub-3-plex-nerviae; venae primariae supra impressae subtus prominentes ad marginem approximatae, secundariae sub angulo 70° divergentes, tertiariae obsoletae; capitula florum dense conferta sub-9-flora; flores sessiles 4-meri; hypanthium tubuloso-campanulatum 3.7 mm. longum minutissime puberulum, pilis adpressis fulvis; calyx primum ovoideo-conicus corollam includens usque 1.4 mm. longus, ad anthesin in lobos 2-4 scariosos irregulariter ruptus; petala obovata 3.2 mm. longa 2.3 mm. lata obtusa glabra aequilatera obscure 5-nervia; stamina isomorpha; filamenta glabra erecta 2.9 mm. longa basi dilatata basi contigua et annulum circum torum formantia; antherae subulatae arcuatae 4.6 mm. longae, poro ventro-terminali dehiscentes, thecis infra medium convolutis, connectivo in medio antherae paucisetoso, basi in calcar 0.5 mm. longum minute setosum producto; ovarium liberum ellipsoideum 2.3 mm. longum glabrum 4-loculare; stylus gracilis glaber 8.5 mm. longus, stigmate punctiformi.

Type, *Klug 3298*, collected at Zepelacio, near Moyobamba, Dept. San Martín, Peru, alt. 1100-1200 m., and deposited in the Britton Herbarium. The species of *Graffenrieda* greatly need reclassification. Among those

published, *G. laurina* Triana is possibly the most similar to ours, but differs in its wider leaves, much larger flowers, definitely lobed calyx, and general habit.

Miconia leucantha Gl. sp. nov. Sect. Tamonea: arbor usque 18 m. alta; rami fistulosi juventute 4-angulati leviter sulcati minutissime cinereo-furfuracei demum teretes glabri; petioli graciles 3-5 cm. longi minutissime cinereo-furfuracei; laminae membranaceae virides ovato-ellipticae, usque 15 cm. longae 8 cm. latae, in caudam linearem obtusam 2 cm. longam 2 mm. latam angustatae, basi obtusae vel subrotundae, 5-nerviae, utrinque glabrae; venae primariae supra planae subtus elevatae saepe rubescentes, secundariae fere rectae, sub angulo fere recto divergentes; panicula late pyramidata, 8 cm. longa, axi ramisque 4-angulatis sulcatis minutissime stellato-furfuraceis; pedicelli crassi 1 mm. longi; flores 5-meri; hypanthium campanulatum 3 mm. longum stellato-furfuraceum; calycis tubus 0.4 mm. longus, lobi late depresso-ovati e sinibus angustis 1 mm. longi, extus furfuracei; petala extus cinerea furfuracea, intus glabra rubescentia, oblique ovata, 5.5-6 mm. longa, oblique truncata vel retusa, latere longiore saepe acuta; stamina paulo dimorpha; filamenta 5.3 vel 6 mm. longa, usque ultra medium dense glanduloso-puberula; antherae subulatae paulo curvatae, 4.8 vel 5.7 mm. longae, poro minuto terminali dehiscentes, thecis paulo convolutis, connectivo basi minutissime bilobo, in ser. ext. dorso glandulis 3-4 stipitatis ornato; ovarium fere superum 3-loculare truncato-conicum minutissime puberulum; stylus fere rectus 10 mm. longus, usque ultra medium dense glanduloso-puberulus; stigma capitatum.

Type, *Skutch 2500*, collected in the vicinity of El General, Prov. San José, Costa Rica, alt. 1010 m., and deposited in the Britton Herbarium. *M. leucantha* is clearly closely related to *M. caudata* (Bonpl.) DC., which it resembles in general habit and in most of its structural features. The pubescence of each consists of minute stellate hairs, which in *M. caudata* are twice as large, more densely crowded, and especially developed on the lower side of the leaves, where they form a continuous brown indument; in *M. leucantha* the leaves are strictly glabrous beneath. The petals of *M. leucantha* are nearly twice as large as those of *M. caudata*, and its filaments and styles are densely glandular; in *M. caudata* both filaments and styles are nearly glabrous. The anthers of *M. leucantha* are slightly larger and in one series bear a few stalked glands on the back.

Miconia flaviflora Gl. sp. nov. Sect. Tamonea: arbuscula 8 m. alta; ramuli juniores primum leviter obtuseque 4-angulati ferrugineo-furfuracei, mox subteretes et glabri; petioli 12-22 mm. longi crassiusculi supra canaliculati subtus rotundati fere glabri; laminae subcoriaceae oblongo-ovatae 10-15 cm. longae 3.5-5.5 cm. latae, breviter sed argute caudato-acuminatae, integrae, basi acutae vel subcuneatae, 3-pli-nerviae, jugo minore submarginali neglecto, supra glabrae opacae, subtus brunnescentes minutissime stellato-lepidotae;

venae secundariae rectae 3–4 mm. dissitae, sub angulo ca. 75° divergentes, supra planae subtus conspicue elevatae; venulae utrinque fere obsoletae; inflorescentia paniculata 10–15 cm. longa multiflora, axibus 4-sulcatis tenuiter brunneo-lepidotis; flores 5-meri in cymulis paucifloris terminalibus dense conferti et sessiles; hypanthium campanulatum ad torum 2 mm. longum, supra ovarium leviter angustatum, tenuiter stellato-lepidotum; calyx ca. 1 mm. longus, velut hypanthio pubescens, mox irregulariter ruptus in lobos 5 triangulares ca. 0.5 mm. longos; petala anguste oblongo-obovata obtusa 3.5 mm. longa 1.2 mm. lata, ad anthesin reflexa extus minutissime puberula; filamenta glabra 2.2 mm. longa; antherae fere isomorpha crasse lineares leviter arcuatae, majores 2.8 mm. longae connectivo basi truncato, minores 2.3 mm. longae connectivo basi brevissime 3-lobato; ovarium inferum 5-loculare; stylus glaber; stigma subcapitatum.

Type, *Klug 3697*, collected at Zepelacio, near Moyobamba, Dept. San Martin, Peru, and deposited in the Britton Herbarium. In its leaf-habit, venation, pubescence, elongate petals, and anthers *M. flaviflora* is undoubtedly close to *M. acuminifera* Triana. Early collections of the species, all in bud, were reported by me as the latter species in 1931 (Bull. Torrey Club 58: 226). Flowering material shows that the petals of *M. flaviflora* are only half as long as those of *M. acuminifera* and that the calyx is much more deeply lobed.

Miconia semisterilis Gl. sp. nov. Sect. Glossocentrum: arbuscula 8 m. alta; rami superiores acute 4-angulares et 2-sulcati dense adpresseque brunneo-lepidoti demum glabrescentes; petioli crassi angulati ca. 1 cm. longi lepidoti; laminae papyraceae anguste ellipticae usque ad 17 cm. longae 6 cm. latae utrinque acuminatae integrae supra glabrae opacae subtus dense cinereo-lepidotae 5-pli-nerviae, jugo exteriore submarginali, jugo interiore ca. 1 cm. ultra basin divergente; venae supra leviter impressae, subtus prominulae; venae secundariae sub angulo 70° adscendentes inter se 3–5 mm. dissitae, tertiariae subrectae vix reticulatae supra obscurae; panícula terminalis 8–10 cm. longa ramosa multiflora lepidota, rhachidibus valde angulatis; flores 5-meri sessiles; hypanthium hemisphaericum 1.1 mm. longum dense lepidotum; calycis tubus 0.3 mm. productum erectum lobis vix evolutis dentiformibus; petala alba obovato-oblonga 1.8 mm. longa 1.6 mm. lata inaequilateraliter truncata glabra; stamina fere isomorpha; filamenta gracilia 1.6 mm. longa; antherae 1.5 mm. longae infra medium steriles ultra medium fertiles obovato-dilatatae 2-loculares poro magno terminali dehiscentes; connectivo infra insertionem filamentum in lobos 2 minutos laterales et lobum 1 (rariter 2) dorsalem anguste oblongum productum; ovarium $\frac{2}{3}$ liberum, ut videtur 3-loculare, summo ovoideo glabro, ovulis ca. 12; stylus crassus 2.6 mm. longus glaber, stigmate truncato 0.5 mm. diam.

Type, *Klug 3224*, collected in forest at Pumayacu, Dept. Loreto, Peru,

and deposited in the Britton Herbarium. The peculiar anthers, sterile for more than half their length and somewhat obovate in the terminal fertile portion, characterize the species and suggest an affinity with *M. Pilgeriana* Ule and *M. stellipilis* Cogn. All three agree further in the appendages of the connective. I have previously offered the opinion that these last two, described originally in the section *Cremanium*, probably belong rather in *Glossocentrum*. Our species differs from these two in its sharply angled stem and lepidote indument. In the last feature it suggests *M. Klugii* Gl., in which the anthers are fertile nearly to the base.

Miconia longisepala Gl. sp. nov. Sect. Amblyarrhena: arbuscula glabra 5 m. alta; rami superiores graciles leviter 4-angulati ad nodos vix incrassati, internodiis 1-2 cm. longis; petioli graciles 10-15 mm. longi; laminae firmulae ellipticae 6-8.5 cm. longae, 2.5-3.5 cm. latae, anguste abrupteque acuminatae in cuspidem linearem 10-15 mm. longam, integrae, basi in petiolum cuneatae, 3-nerviae (jugo obscuro marginali neglecto); venae primariae supra leviter impressae subtus prominulae in acumine approximatae, secundariae utrinque planae subflexuosae sub angulo 60-70° adscendentes, tertiariae supra obsoletae subtus reticulatae; panicula ramosa vix pedunculata 7 cm. longa, ramis oppositis 2-3-floris; pedicelli graciles, ut videtur circa 8 mm. longi sed infra flores nodosi et pedicelli veri tantum 0.5 mm. longi; flores 5-meri; hypanthium subglobosum 3.5 mm. longum rugulosum; calycis tubus vix evolutus, lobi patuli vel reflexi lineari-oblongi 3.2 mm. longi acuti, dentibus exterioribus linearibus teretibus 0.8-1.0 mm. longis sepala subaequantibus et ad sepala arcte adpressis; petala reflexa late oblonga 5.6 mm. longa 3.6 mm. lata inaequilateraliter retusa; stamina fere isomorpha inter se paulo variabilia; filamenta crassa complanata 2.7-3.4 mm. longa dense glandulosa praecipue prope apicem glandulis subsessilibus; antherae semi-ovoideae 2.4-3.0 mm. longae 4-loculares poro minuto ventro-terminali dehiscentes, connectivo simplici; ovarium semi-inferum 5-loculare, parte libera conica glabra 10-sulcata; stylus crassus 8 mm. longus glandulosus, glandulis infra medium minimis brevissime stipitatis, prope apicem majoribus subsessilibus; stigma rotundato-peltatum, 2-3 mm. diam.

Type, *Klug 3233*, collected in forest at Pumayacu, Dept. Loreto, Peru, alt. 600-1200 m., and deposited in the Britton Herbarium. In its general habit and inflorescence and especially in its glandular stamens and style, *M. longisepala* shows its affinity to a group of ten Andean species, of which *M. floribunda*, *M. majalis*, *M. macrantha*, and *M. grandifolia* are probably best known. It is the only species of the group, as far as known to me, with distinctly 3-nerved leaves and it differs from the rest still more notably in the remarkably long sepals which nearly equal the hypanthium.

Miconia expansa Gl. sp. nov. Sect. Amblyarrhena: frutex 3 m. altus; rami superiores exacte 4-angulares glabri, nodis superne sensim dilatatis; petioli

crassi quam laminis 5-8-plo breviores; laminae membranaceae obovato-oblongae breviter abrupteque apiculatae (apiculo 2-5 mm. longo anguste triangulari) integrae sparse glanduloso-ciliatae (pilis 0.5 mm. longis saepe incurvis) basi late cuneatae utrinque glabrae 5-ply-nerviae, jugo obscuro marginali neglecto, venae supra planae obscurae; venae secundariae sub angulo ca. 70° adscendentibus inter se 2-4 mm. dissitae subtus planae, tertiariae supra obsoletae subtus arcte reticulatae; panicula terminalis ampla 16 cm. longa, fere glabra tantum ad nodos sparsissime furfuracea, ramis 7 a nodo superiore, quorum jugo infimo 4 cm. longo paucifloro, terminale elongato multifloro; rami paniculae saepissime 2 in quoque latere a nodis superioribus, superiores oppositi, omnes superne sensim dilatati et valde 4-alati; ramuli supremi breves 1-flori, pedicello tereti brevissimo; hypanthium campanulatum carnosum glabrum 4 mm. longum; calycis tubus non evolutus; sepala ad torum distincta suberecta late ovata glabra 2 mm. longa fere totidem lata, ad apicem obtusam brevissime glanduloso-setosa; petala carnosae alba rotundato-ovata 4.7 mm. longa 4 mm. lata; stamina isomorpha; filamenta crassa erecta complanata 3 mm. longa prope apicem pauciglandulosa; antherae semiovoideae 2.7 mm. longae 4-loculares; connectivum simplex prope basin nonnunquam pauciglandulosum; ovarium inferum 5-loculare, parietibus internis minute foveolatis, summo radiatim costatum et circum stylum depressum; stylus crassissimus 5.6 mm. longus, stigmatum capitato 1.8 mm. lato.

Type, *Klug 3201*, collected in forest at Pumayacu, Dept. Loreto Peru, alt. 600-1200 m., and deposited in the Britton Herbarium. This is another member of the same group typified by *M. floribunda* and *M. grandiflora*, and differing from all of them in the conspicuously winged branches of the inflorescence.

NEW YORK BOTANICAL GARDEN

INDEX TO AMERICAN BOTANICAL LITERATURE 1931-1936

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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